University of Alberta

Pileated Woodpecker Habitat Ecology in the Alberta Foothills

By

Richard Lloyd Bonar

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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Abstract

Little is known about pileated woodpecker (*Dryocopus pileatus*) habitat ecology in western boreal cordilleran forests. To evaluate these relationships, I conducted a 5-year study near Hinton in the foothills of west central Alberta, with additional information about cavity trees collected from a larger area. I evaluated habitat use in 14 pileated woodpecker pair territories at territory, stand, site, substrate, and substrate position scales using radiotelemetry and direct observation. Pileated woodpeckers used all available habitat at all scales examined. Large wood foraging substrates containing carpenter ants (*Camponotus spp*) and cavity trees with stem decay, especially trembling aspen (*Populus tremuloides*), were selected and small substrates and healthy trees were avoided. Habitat use and selection were strongest at the substrate and position scales. Pair territories averaged 2,156.6 ha in size, which was more than 4 times larger than reported in previous studies. Territory size was inversely related to density of potential foraging substrates and cavity trees. Habitat variables and territory size were not related to adult survival and productivity, which were the highest reported for pileated woodpeckers. Territories contained 4–48 cavity trees. There was an average of 2.2 cavities/km^2 and cavity production exceeded cavity loss during the study period. There was an apparent surplus of cavities available during all seasons. Of those cavities inspected, 44.6% were used by pileated woodpeckers, >18 other species used 66.6%, and 22.3% were empty. Pileated woodpeckers used all available habitats at the territory and stand scales and they selected large dead and damaged trees at the substrate and position scales. They are not mature or old forest obligates, but they may be good indicators for ecological function. Pileated woodpecker cavities are an important resource for cavity-using wildlife in western forests, and they may be a critical resource for large secondary cavity-using species that are too large to enter cavities excavated by smaller woodpeckers. Forest managers should conserve existing dead wood resources and reserve living trees to provide future living trees and dead wood suitable for pileated woodpecker use. Existing pileated woodpecker cavity trees should be protected and strategies should be implemented to support continued production of new cavity trees.

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1. INTRODUCTION

The pileated woodpecker (*Dryocopus pileatus*) occurs in North American forests from northern British Columbia to central California in the west, across southern Canada, and from Nova Scotia to southern Florida in the east (Bull and Jackson 1995). In Alberta, pileated woodpeckers occur mainly in the Boreal Forest, Foothills, and Rocky Mountain Natural Regions, and they were recorded in 15.3% of the 100-km^2 squares (n = 2,206) surveyed for the Alberta Breeding Bird Atlas (Semenchuk 1992).

Although about half of the range of pileated woodpeckers is in Canada, published ecological information comes mostly from the United States (Bull and Jackson 1995, Kirk and Naylor 1996). Recent U.S. research was primarily in the Pacific Northwest (Bull et al. 1992, Mellen et al. 1992, Bull and Holthausen 1993; Aubry and Raley 1992, 1995). Prior to 1990, general distribution notes and nest records were the only available information on pileated woodpeckers in Canada (eg Peck and James 1983, Dance 1987, Wedgwood 1988, Harestad and Keisker 1989, Campbell et al. 1990). Since, research projects were initiated in Manitoba (Millar 1992), Quebec (Savignac 1996), New Brunswick (Flemming et al. 1999), British Columbia (Hartwig 1999), Ontario (Bush 1999) and Alberta (this study). Radiotelemetry was used to investigate pileated woodpecker habitat relationships in 7 previous studies (Mannan 1984; Renken and Wiggers 1989, 1993; Aubry and Raley 1992, 1995; Bull et al. 1992; Mellen et al. 1992; Savignac 1996; Watts et al. 1998).

Little is known about pileated woodpecker habitat ecology in northern boreal and cordilleran forests. Differences between these forests and southern forests where most pileated woodpecker research has been conducted are substantial. There are fewer tree species, and the average size of trees is smaller. Forest fires are dominant natural disturbances, and large fires are the major source of disturbance. Winters are longer and colder, with extensive periods of snow cover. Because of these differences and knowledge that pileated woodpecker habitat ecology differs among other forest regions where the species has been studied (Bull and Jackson 1995, Kirk and Naylor 1996), relationships observed elsewhere may not be valid in northern boreal and cordilleran forests.

LITERATURE REVIEW

The pileated woodpecker may form a superspecies with the lineated woodpecker (*D. lineatus*) of Central America and northern South America and the black-bodied woodpecker (*D. schulzi*) of southern South America (Short 1982). There are 3 other *Dryocopus* species: (1) the black woodpecker (*D. martius*) in Europe; (2) the white-bellied woodpecker (*D. javensis*) in Java; and (3) the helmeted woodpecker (*D. galeatus*) in South America (Short 1982, Winkler et al. 1995). With the probable extinction (American Ornithologists' Union 1998) of the world's two largest woodpecker species, the ivory-billed woodpecker (*Campephilus principalis*) and the imperial woodpecker (*C. imperialis*), the pileated woodpecker is now the largest North American woodpecker, and the sixth largest in the world (Winkler et al. 1995). Pileated woodpeckers are approximately double the mass of the northern flicker (*Colaptes auratus*), the second largest North American species (Short 1982).

The body mass of adult pileated woodpeckers is 240–350 g, and males are 5–15% heavier than females (Short 1982, Bull and Jackson 1995). Malar coloration visibly distinguishes the sexes (red in males, black in females), and the red crest on top of the head is larger on males. Habitat use by males and females may not be similar, although this has not been studied in detail (Bull 1980, Mellen et al. 1992).

Pileated woodpeckers are single-brooded. Annual clutch size averages 3.83 eggs (range 1–6; Bull and Jackson 1995) and 83% of nests (n = 81) in an Oregon study fledged at least 1 young (Bull and Meslow 1988). The average number of fledglings was 2.0 in Montana (McClelland 1977), 2.14 in Louisiana (Tanner 1942), and 2.26 in Oregon (Bull and Meslow 1988). Fledged young remain with the parents until fall (Hoyt 1957, Bull and Jackson 1995). Pileated woodpeckers breed at age 1 if they can obtain a mate and establish a territory or, more commonly, replace territorial birds that die (Bull and Jackson 1995). Non-territorial birds may

wander or establish themselves as "floaters" within mated pair territories (Bull and Holthausen 1993, Bull and Jackson 1995).

Population turnover is relatively high as 36–67% of adults die each year. Annual adult survival estimated using colour-banded birds was at least 64% in northeastern Oregon (Bull and Meslow 1988). Annual survival estimated using radiotagged birds was 56% in Oregon (Bull et al. 1992), and 43% in Washington (K. B. Aubry and C. M. Raley, cited in Bull and Jackson 1995). Adults have reached the age of almost 10 years in the wild (Hoyt and Hoyt 1951, Hoyt 1952, Bull and Meslow 1988).

Pileated woodpeckers were killed for food, sport and ceremonial purposes until the first several decades of the 20th century (Bull and Jackson 1995, Gauthier and Aubry 1996). Populations have since recovered and are still rising in many areas (Hoyt 1957, Short 1982, Price et al. 1995). Predation is the main cause of adult mortality (Bull and Jackson 1995). Known avian predators are large raptors such as the northern goshawk (*Accipiter gentilis*), Cooper's hawk (*A. cooperii*), red-tailed hawk (*Buteo jamaicensis*), and great horned owl (*Bubo virginianus*; Bull and Jackson 1995). Smaller raptors such as the sharp-shinned hawk (*A. striatus*) are apparently not large enough to take pileated woodpeckers (Kilham 1958). The American marten (*Martes americana*) and gray fox (*Urocyon cinereoargenteus*) are known mammalian predators of adults (Todd 1944, Bull and Jackson 1995). Pileated woodpeckers respond to predator presence by remaining silent and motionless or alternatively by giving alarm calls and moving higher on trees (Bull and Jackson 1995). They avoid predator attacks by (1) jumping to the opposite side of a tree trunk (Lima 1993); (2) flight; or (3) aggressive counter-attack (Michael 1921). Other factors being equal, pileated woodpeckers may select habitat that increases probability of escape from predators (Lima 1993).

Monogamous pairs aggressively defend territories throughout the year against other territorial pileated woodpeckers (Hoyt 1957, Kilham 1976, Bull 1987). In northeastern Oregon, territories were 321–630 ha (407 ± 110.3; $\bar{x}$ ± SE) for 7 pairs radiotracked for 5–10 months, and 200–1,464 ha (597 ± 388.1) for 9 individuals that had lost their mates (Bull and Holthausen 1993). In western Oregon, 11 birds radiotracked up to 3 months in summer had territories of 267–1,056 ha (478 ± 219; Mellen et al. 1992). In Missouri 11 birds radiotracked up to 43 days in summer had territories of 52.9–160.1 ha (87.5 ± 31.6; Renken and Wiggers 1989). Individual territory estimates were approximately 88% of the combined territory of pairs (Bull and Holthausen 1993). In general, pair territories did not overlap with neighbours except temporarily when a bird had lost its mate or adults with fledged young travelled outside their normal territory range (Mellen et al. 1992, Bull and Holthausen 1993).

Pileated woodpeckers usually excavate a new nest cavity every year in the trunk of a large tree (Short 1982, Bull and Jackson 1995). Reuse of old nest cavities is rare (Bull 1987). Although they can excavate in solid wood (Miller et al. 1979, Bull 1987), pileated woodpeckers usually nest in trees partially softened by fungal decay at the cavity site (Conner et al. 1976, McClelland 1977, Bull 1987, McClelland and McClelland 1999). Nests are excavated in large dead or declining living trees of many species (Conner et al. 1975, McClelland 1979, Short 1982, Harris 1983, Bull 1987, Mellen 1987). Selection for tree species, size, and decay characteristics varies across the range of the species and appears to depend mainly on availability of suitable trees (Kirk and Naylor 1996).

Pileated woodpeckers roost each night in tree cavities, which include old nest cavities, natural cavities, and new cavities excavated exclusively for roosting (Downing 1940, Bull et al. 1992, Aubry and Raley 1995). Roosting cavities may provide protection from predators and physiological moderation against the influence of temperature and moisture (Kendeigh 1961, Bull et al. 1992, Kellam 1996), and they may be particularly important for winter survival.

Like other primary cavity excavator species, pileated woodpeckers excavate cavities that are also used by other cavity-using forest wildlife species. For example, 18 of 19 cavities used by nesting boreal owls (*Aegolius funereus*) in an Idaho study were originally excavated by pileated woodpeckers (Hayward et al. 1993). Existing information about availability of pileated woodpecker cavities and use by other species is anecdotal (Hoyt 1948, 1957; McClelland 1977; Bull and Snider 1993; Hayward et al. 1993; Bull and Jackson 1995).

Both sexes drum on standing dead wood, probably to establish and defend territories and as part of the courtship process (Hoyt 1957; Kilham 1959, 1979). Drumming takes place all year, but

especially marks the pre-breeding period, often at particular drumming trees (Short 1982). Repeated use of drumming trees, particularly those near territorial boundaries, may be an important defence against encroachment by neighbouring pairs.

Pileated woodpeckers are strong excavators, and they are the only North American species that makes deep foraging excavations through undecayed wood in search of food (Conner 1979, Bull and Holthausen 1993, Bull and Jackson 1995, Flemming et al. 1999). They also scale bark to obtain the larvae of wood-boring beetles (Bull 1987, Cannings 1987, Kroll and Fleet 1989), and eat plant foods, especially berries and fruits (Beal 1911, Hoyt 1957, Cannings 1987). Pileated woodpeckers feed extensively on wood-boring insects throughout the year (Beal 1911, Hoyt 1957). They specialize on carpenter ants (*Camponotus spp*; Bent 1939, Hoyt 1950, Dater 1953, Beckwith and Bull 1985). Foraging methods change seasonally (Hoyt 1957, Conner 1979, McClelland 1979, Bull 1987). In summer, ants and other insects are obtained by (1) pecking and gleaning on or near the surface of logs, stumps, and standing dead and live trees; and (2) extensive excavations deep into partially decayed wood. In winter ants are obtained by extensive excavating into relatively sound wood at the bases of trees containing carpenter ant colonies (Hoyt 1957, McClelland 1979, Conner 1981, Bull et al. 1986, Flemming et al. 1999). Foraging substrates used by pileated woodpeckers are usually large in comparison to available substrates and vary in species, size, and decay characteristics between study areas (Bull et al. 1986, Bull and Holthausen 1993, Flemming et al. 1999).

Pileated woodpeckers are most often associated with mature or old forests (Conner and Adkisson 1976, Conner 1980, Mellen et al. 1992, Bull and Holthausen 1993, Renken and Wiggers 1993). However, they also use immature forests with residual trees, logs, and stumps from a previous disturbance (Conner and Crawford 1974; Conner et al. 1975, Mellen et al. 1992, Savignac 1996, Shackelford and Conner 1997). Presence and density of large trees for nesting and foraging may be more important than forest age (Kirk and Naylor 1998, Rolstad et al. 1998).

PILEATED WOODPECKER CONSERVATION AND FOREST MANAGEMENT

Sustainable forest management aims to sustain healthy forests while providing benefits for current and future generations, and conservation of biological diversity is a key criterion of sustainable forest management (Canadian Council of Forest Ministers 1995, Environment Canada 1995). Many contemporary forest managers are using a concept of coarse- and fine-filter approaches to conserve biodiversity (Hunter 1990). The Nature Conservancy (Noss 1987) first proposed this approach. The coarse-filter approach maintains a variety of ecosystems and elements of forest structure, composition, and function at a variety of scales, assuming that a representative array of ecosystems will sustain the vast majority of species in a region. The Nature Conservancy estimated that 85-90% of species would be conserved with the coarse-filter approach (Noss 1987). The fine-filter approach is directed towards conservation measures for individual species that fall through the pores of the coarse filter. The original concept of the fine-filter approach was directed only at species known to be at risk (Hunter 1990). In the fine-filter component of a biodiversity conservation strategy, management actions are usually focussed on several important species. Importance can be subdivided into three components: economic importance, for species exploited by humans; ecological importance, for species with key ecological roles; and social importance, for species that may be at risk. Species importance is commonly ranked using evaluation criteria (eg Bonar et al. 1990, Millsap et al. 1990, Alberta Natural Resources Service 1996, Kuhnke and Watkins 1999). Managers select species that best represent importance issues in their area.

A number of Canadian forest biodiversity conservation programs have selected the pileated woodpecker as an important focus species (Bonar et al. 1990; Bull et al. 1990, 1992; Koven and Martel 1994; Saskatchewan Forest Habitat Project 1991, Watts et al. 1998, Kuhnke and Watkins 1999). The main reasons for selection were concerns about the long-term effects of timber management on pileated woodpeckers, and recognition of the key ecological role that they may play in conservation of cavity-using wildlife communities. In northern forests, where large natural cavities may be rare, a continuing supply of old pileated woodpecker cavities could be particularly important for large cavity-using wildlife species that cannot enter cavities made by smaller woodpeckers.

Because they need large trees for nesting and roosting and forage primarily on dead or declining wood substrates, long-term conservation of pileated woodpecker populations may depend on maintaining these key structural elements in forest landscapes (Bull 1987, Bull and Jackson 1995). Large dead and declining trees are associated mainly with mature and older forests (McClelland 1979, Bull 1987, Renken and Wiggers 1989, Mellen et al. 1992). However, they are also found in young forests as remnant structure following a natural disturbance or logging. Although use of younger forests with remnant structure has been documented, many authors consider that young or fragmented forest habitat may not sustain pileated woodpeckers (Robbins et al. 1989, Bull and Holthausen 1993, McClelland and McClelland 1999). Others believe that pileated woodpeckers may be able to prosper in young and fragmented forests with abundant remnant structure (Mellen et al. 1992, Savignac 1996, Rolstad et al. 1998).

In addition to their ecological role as predators of wood-dwelling forest ants, especially carpenter ants, pileated woodpeckers are thought to fill a keystone function (Power et al. 1996) as producers of large tree cavities that support cavity-using wildlife communities (Hoyt 1957, McClelland 1977, Bull and Snider 1993, Bull and Jackson 1995). Although there are numerous anecdotal accounts of secondary cavity-users using pileated woodpecker cavities, there have been no quantitative studies.

Relative rarity, association with late seral forests, and ecological importance justify concerns about the long-term effects of timber management on pileated woodpeckers. This concern, together with the poor understanding of pileated woodpecker ecology in western boreal and cordilleran forests, was the catalyst for my research to gather knowledge that could be used to determine habitat conservation strategies and incorporate them into forest management planning.

RESEARCH QUESTIONS

Ecological theory holds that the fitness of an individual will increase as the quality of occupied habitat increases. Fitness is related to survival and reproduction of an individual and habitat quality is related to the ability of an individual to obtain essential life requisites from its environment. Animals living in high quality habitat should have high relative rates of survival, reproduction, and vitality of their offspring, when compared to animals living in low quality habitat (Van Horne 1983, Morrison et al. 1992). Relationships between habitat quality and species fitness have both theoretical and practical significance because they can be used to predict species response to changes in habitat quality (Kennedy and Gray 1993).

In wildlife ecology the concept of habitat selection refers to the relative proportion of activity-dependent use of habitat units compared to the relative availability of habitat units. Use depends on activity type and must be defined for each measure of habitat selection. The null hypothesis is that use is proportional to available habitat (no selection). Positive selection occurs when an animal uses a habitat unit more often than expected and negative selection occurs when an animal uses a habitat unit less often than expected.

Animals select habitat at various scales and may show selection at some scales but not others (Johnson 1980). An example is shown for pileated woodpecker nest trees in Table 1.1. For reproduction to occur, a territory must contain at least some trees suitable for nesting. One of the factors governing territory location at a landscape scale must therefore be the presence of potential nest trees. Within a territory, pileated woodpeckers may select particular types of forest stands (areas of relatively distinct vegetation when compared to other adjacent areas), particular types of very local sites within stands, particular trees within sites, and particular locations on trees. Alternatively, birds may select trees and locations on trees and show no selection for sites or stands.

Table 1.1. Habitat selection scale hierarchy example - reproduction.

Scale	Description	Size	Selection
Territory	Area occupied by a mated pair	>1000 ha	Contains suitable nest trees
Stand	Area of similar vegetation	2-100 ha	Area containing nest tree
Site	Local area within stand	<0.5 ha	Immediate area of nest tree
Element	Individual tree or other substrate	Tree	Tree containing nest cavity
Sub-element	Location on substrate	Position	Location of nest cavity

In this study I investigated relationships between habitat quality and fitness-related response of pileated woodpeckers in Alberta foothills forests. Habitat quality aspects of the study were trees used for nesting and roosting and the type, density and interspersion of foraging substrates. Fitness response aspects were habitat selection, territory size, reproductive success, and adult survival. Habitat selection was defined as the scale-dependent use of habitat by pileated woodpeckers compared to the availability of habitat, expressed as a ratio of use/availability. I also studied the ecological role of the pileated woodpecker as a producer of large tree cavities by investigating the availability of pileated woodpecker cavities and their use by other species.

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2. PILEATED WOODPECKER HABITAT USE AND SELECTION IN THE ALBERTA FOOTHILLS

Pileated woodpeckers defend territories throughout the year against neighbouring pairs (Bull and Jackson 1995). Although widely distributed, the pileated woodpecker is never abundant, with individual home ranges of 257–1,464 ha (Renken and Wiggers 1989, Mellen et al. 1992, Bull and Holthausen 1993). Pileated woodpeckers are strongly linked to trees, especially dead trees, logs, stumps, and living trees with defects (Bull and Jackson 1995). Pileated woodpeckers nest and roost in cavities excavated in large trees (Hoyt 1957, McClelland 1977, Bull 1987, Bull et al. 1992a). They prey on wood-dwelling insects, especially carpenter ants (*Camponotus spp*), obtained mainly from dead wood (Conner 1981, Mannan 1984, Bull and Holthausen 1993), and use trees to escape avian predators (Lima 1993).

The pileated woodpecker is a management indicator species for mature/old forest conditions in some U.S. National Forests (Bull and Holthausen 1993). In Canada, the pileated woodpecker is a species of special interest in many provinces (Kirk and Naylor 1996), primarily because of concerns about the effects of forest management, which may reduce availability of key structural components of pileated woodpecker habitat. Pileated woodpeckers occur across the southern belt of the North American boreal forest, but little is known about their habitat ecology in western boreal and cordilleran forests (Harestad and Keisker 1989, Millar 1992), which have generally smaller trees and longer winters with more snow cover compared to southern forests. I studied key aspects of pileated woodpecker habitat selection in the Alberta foothills at several scales to obtain ecological information needed to support forest management planning. I focussed on foraging ecology and cavity tree selection within pair territories, at the levels of third- and fourth-order selection (Johnson 1980). I defined selection at 5 scales: (1) within the territory of each bird or mated pair; (2) within stands in each territory; (3) at sites within stands; (4) at wood substrates used by birds; and (5) at the position used on the substrate.

STUDY AREA

The study area was the 26,000-km^2 Foothills Model Forest in the Rocky Mountain and Foothills Natural Regions (Beckingham et al. 1996) of west central Alberta, Canada. Cavity tree information was also obtained on an opportunistic basis from forested areas of central Alberta and British Columbia. This area was roughly bounded on the west by Prince George, on the north by Fort McMurray, on the south by Red Deer, and on the east by the Alberta-Saskatchewan border. Most information was obtained within 14 territories of radiotagged pairs of pileated woodpeckers within approximately 50 km of Hinton, Alberta (127°46'N, 117°39'W). Forests above 1,150 m were dominated by lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*). Below 1,150 m, mixed forests were codominated by lodgepole pine, trembling aspen, white spruce (*P. glauca*), and balsam poplar (*Populus balsamifera*; Beckingham et al. 1996). Other common tree species included black spruce (*P. mariana*), tamarack (*Larix laricina*), and subalpine fir (*Abies lasiocarpa*). Forest age composition was 12% <30 years, 30% 31–100 years, 52% 101–160 years, and 6% >160 years (Weldwood of Canada, unpublished data).

METHODS

Radiotelemetry

I radiotagged and followed 32 adult pileated woodpeckers and 1 juvenile in 14 pair territories from June 1993–June 1996. Birds were initially captured in 1993 (n = 2), 1994 (n = 16), and 1995 (n = 15) at nest trees (n = 28) or roost trees (n = 4), using a hoop net or board trap (Bull and Pedersen 1978). Each bird was fitted with an 11-g, 2-stage transmitter attached with a backpack harness. Birds were recaptured to replace transmitters when batteries failed at 5–12 months. I radiotagged both pair members in 12 territories and 1 bird in 2 territories. When birds died, I radiotagged new birds that replaced them. Birds were followed for 3 years in 2 territories, 2 years in 12 territories, and 1 year in 2 territories. Individuals were followed over periods of 9–763 days

(n = 6,120 locations, range 6–488 locations/bird). Transmitters were removed in June 1996 from all birds except 3 that could not be recaptured because their transmitter batteries had failed.

A single observer followed each radiotagged bird in daylight hours between roost emergence and roost entry for approximately 4 hours at intervals of 2–10 days. The observer used homing (Mech 1983) to move within 50 m and establish visual or aural contact without disturbing the bird, or alternatively to estimate the bird location to within approximately 15 m. The observer waited until the bird moved to another location, and then measured substrates used by the bird before resuming the follow. Observations were interrupted until the observer could re-establish contact if the bird was disturbed by the observer or flew far away. On each follow, the observer attempted to obtain data for at least 10 separate bird locations, which were classified as visual (bird observed), aural (bird heard), site (foraging site located), or radio (location only).

Once contact was established, the time was recorded to the closest minute at the start and end of each activity or bird movement. If the bird was visible or activity could be determined using sound or site inspection, time was allocated to foraging, resting, interaction with other pileated woodpeckers (calling, drumming, courtship, juvenile and neighbour interactions, etc), and other (preening, flying, cavity excavation, nesting duties, roosting, etc). Foraging was classified as searching or gleaning on the wood surface, pecking or scaling bark, and excavating into sapwood.

Tree species and type (live, snag (dead tree with intact trunk), stub (dead tree with broken trunk), stump (cut with saw), log) were determined for each used wood substrate. Diameter at breast height (dbh) was measured 1.3 m above the base for trees, snags, stubs and logs ≥1.3 m, and diameter was measured at the top for stumps, stubs, and logs <1.3 m tall. Height or length to the closest 0.1 m was estimated using a clinometer or measured with a tape measure for stubs, stumps, and logs. For dead wood types, bark cover: (1) <25%; (2) 26–50%; (3) 51–75%; and (4) >75%), and decay class: (1) recently dead, wet inner bark, sap and foliage often present; (2) dry stem and bark, fine branches present, bark present and firmly attached; (3) mostly sound stem, fine branches gone, main branches present, bark variable; (4) few or no branches, softening stem, variable bark; (5) no branches, stem soft, bark mostly gone; and (6) stem shape intact, no branches, bark gone, stem very rotten, were estimated. Decay classes were grouped into hard (decay classes 1–3) and soft (classes 4–6) categories. Presence and type of visible decay indicators were recorded for live trees. Fungal conks were considered to be conclusive decay evidence. Strong decay indicators were large dead branches or branch stubs, and trunk cracks, crooks, or swellings. Weak decay indicators were dead, forked or broken tops, and scars, galls, or injuries. Presence and position of previous pileated woodpecker excavation evidence was noted and classified as recent (within several days), fresh (within current season) or old based on the position of wood chips in relation to snow, rain, or litterfall, and wood weathering or sap extrusion at the excavation site. I recorded bird position as: (1) root; (2) base = ≤2 m from bottom; (3) top = ≤2 m from top; (4) trunk = >2 m from bottom or top; (5) branch; or (6) ground. The height of the bird above the substrate base was estimated to the closest 2 m. Foraging sites were inspected for visible food items: (1) carpenter ants; (2) thatching ants (*Formica* spp); (3) other ants (*Formicidae*); (4) other arthropods; and (5) unknown (no visible food items).

Cavity Trees

A cavity was defined as any opening excavated by pileated woodpeckers into a tree with entrance dimensions similar to those of completed nest cavities. Cavity trees were located by following unmarked and radio-tagged pileated woodpeckers, searching, listening for adult and nestling calls, and reports from the public. I attempted to locate all cavity trees within 14 territories by following radiotagged pileated woodpeckers and searching, with total effort equivalent to 2,022 8-hour person-days. Radiotagged birds often visited cavity trees during the day and always roosted in cavity trees at night. Searches for cavity trees in 1993, before birds were radiotagged, were conducted by walking parallel transects in a grid pattern, with systematic coverage of all areas searched. This method was inefficient, so in 1994–98 I used aerial photos and forest inventory information to identify stands in territories that were likely to contain large living or dead trembling aspen or balsam poplar trees and large conifer snags. These trees were identified as most likely to have pileated woodpecker cavities based on 1993 surveys. I was not able to search

all likely stands, but I did search >75% of those identified in each territory; total effort ranged from 64–306 days/territory, and 11 of 14 territories received ≥115 days of effort. Cavity trees found using radiotelemetry were similar to trees found using other methods, so all cavity trees found within the study area were used in the analysis.

For each live cavity tree, I determined species, type, dbh, height, height to base of crown, and presence of decay indicators using the same criteria used to measure foraging substrates. For dead trees, I also measured decay and bark class. I used a ladder or climbing spurs to access cavities in 62% of cavity trees. For each cavity, I measured height of the entrance above ground, tree diameter at cavity entrance, entrance orientation, and distance to the closest decay indicator. On an arbitrary sample of 252 cavity trees I measured the height of all decay indicators and the distance from 2 random heights to the closest decay indicator.

Habitat Characterization at the Territory and Stand Scales

All telemetry and cavity tree locations were marked on 1:15,000 aerial photos, transferred to maps of the same scale, digitized, and linked to a corresponding database record. A Geographic Information System (GIS) containing vegetation and base features inventory (Weldwood of Canada Ltd., unpublished data) was used to determine attributes (see description below) for each location: forest type; seral stage; stand information (tree species composition to closest 10%, height to closest m, area in ha, canopy closure, age); elevation; slope; and aspect. Vegetation information conformed to the Alberta Vegetation Inventory standard (Nesby 1997).

To determine habitat availability I assessed habitat characteristics within the minimum convex polygon (MCP; Mohr 1949) area encompassing all birds within each territory over: (1) the nesting period (May 1–June 30) in each year; (2) each year beginning June 1 and ending May 31 (year 1 = 1993–94, year 2 = 1994–95; year 3 = 1995–96); and (3) the total telemetry monitoring period. June 1 was selected as the start of the monitoring period because this was the approximate date that eggs hatched and adults were radiotagged. I excluded from the MCP calculations 17 locations for 2 birds that temporarily left their territories. Territory size for pairs and individual birds with >50 locations/year was stable between years.

For territory-scale analysis, stands within each MCP area were classified into 6 forest types (1) pine = ≥50% lodgepole pine, <20% deciduous; (2) upland spruce = ≥50% white spruce or subalpine fir, <20% deciduous; (3) lowland spruce = ≥50% black spruce or tamarack, <20% deciduous; (4) deciduous = ≥80% aspen or balsam poplar; (5) mixed = ≥20% each coniferous and deciduous; and (6) non-forest = <6% forest cover (water, non-vegetated, grass, shrub, settlements). Tamarack was considered to be a coniferous species. Each type was classified into 4 seral stages based on stand age. Seral stages for coniferous types (pine, upland spruce, lowland spruce) were (1) young (<30 years); (2) pole (31–100 years); (3) mature (101–160 years); and (4) old (>160 years old). Seral stages for deciduous and mixed types were young (<30 years), pole (31-80 years), mature (81–120 years), and old (>120 years). Forest type categories corresponded to major ecological ecosite and ecosite phases from the ecological classification for the area (Beckingham et al. 1996). Seral stage categories corresponded to major structural changes associated with forest succession for the area (Weldwood of Canada Ltd., unpublished data). Examination of plots of stand composition and age compared to use showed that use-availability analyses were not sensitive to forest type and seral stage category definitions.

For stand-scale analysis, habitat characteristics within stands in each territory were quantified using GIS analysis of vegetation to determine tree species composition, height, age, and canopy closure. Availability for polygonal variables was determined by calculating the proportion of each category within the respective MCP area. Availability for point variables (elevation, slope, aspect) was determined by generating 500 random points within each composite MCP territory (n = 7000).

Habitat Characterization at the Site, Substrate, and Substrate Position Scales

I used fixed-area plots to sample available sites and trees for cavity tree analysis and wood substrates (trees, snags, stubs, logs, and stumps) for habitat analysis. Substrates were measured

if ≥0.5 of the base was within the plot. For cavity tree analysis, all live trees, snags, stubs, stumps, and logs ≥10 cm diameter at the top (stumps, stubs, and logs <1.3 m height), or breast height (trees, snags, stubs, and logs ≥1.3 m) were measured in 504 0.04 ha circular plots. Half of the plots were centred on arbitrarily selected cavity trees. Each of these was paired with a plot located using a random numbers table to repeatedly select a compass bearing and distance (measured by pacing) from the cavity tree until the plot location fell within the cavity-tree stand and did not overlap with the cavity tree plot. Random plots were centred on the closest tree to the paced plot location. Each plot was divided into quarters using cardinal compass bearings. I calculated an openness index by measuring the distance from the cavity or centre tree to the 2 closest trees in each quarter and summing the total. For habitat analysis, I used data for live trees and snags ≥10 cm dbh from 3,000 permanent 0.8 ha square plots systematically located in the corners of a 1.6 km^2 grid covering a 1 million ha area that encompassed the pileated woodpecker territories (Weldwood of Canada, unpublished data). From these, I randomly selected 25 plots from each forested (≥6% canopy closure) forest type for the pole, mature, and old seral stages (n = 375 plots). Data for stubs, logs, and stumps was not available from permanent sample plots, so I used data for these substrate types from random plots established for cavity tree sampling (n = 74) and an additional 126 0.04 ha plots located within territories, for a total of 10 plots for each type/stage combination (n = 200). The extra plots were randomly selected from type/stage maps and located by pacing along compass bearings from reference points visible on aerial photographs. I estimated availability of substrates by multiplying proportions or means derived from the plot data for the total area sampled by forest type and seral stage times the proportion of each type/stage combination in each MCP area.

Statistical Analyses

I used 95% simultaneous confidence intervals for multinomial proportions (Bailey 1980) to determine if pileated woodpeckers selected categorical habitat variables disproportionately at different scales. The Bailey (1980) intervals performed better than binomial intervals (Byers et al. 1984) in a comparison test (Cherry 1996). I did not conduct power analyses, but sample sizes for most comparisons were sufficient to yield statistically significant differences between proportions that differed by 1–5 %, so it is unlikely that biologically relevant differences were missed because of low power. I used paired t-tests and ANOVA to compare average values for the variables used by pileated woodpeckers to the average values of variables for available habitat at different scales. I compared observed use of variables in summer (April–September) and winter (November–February) with their proportional abundance for: (1) all birds compared to the sum of available habitat in all 14 territories; and (2) all birds within each territory compared to available habitat within each territory. Each comparison was conducted by comparing observed use to available habitat using: (1) cumulative MCP area; (2) annual MCP area; and (3) nesting season MCP area. I used chi-square tests to compare male and female habitat use between years within each territory and all males compared to all females.

RESULTS

Habitat Selection at the Territory and Stand Scales

From 1993–1996, I obtained 7,189 locations and observed 36 (radiotagged n = 32) pileated woodpeckers in 14 territories for a total of 52,138 minutes. Birds spent 85.9% of their active time foraging, and did not use different habitats for foraging and other activities except for nesting and roosting, which were focussed on stands with cavity trees. Habitat use between sexes and between years did not differ, so data were combined for subsequent analyses. Analyses using all radiotagged birds were generally similar to analyses comparing territories (n = 14) and individuals (n = 20), although there was considerable variation. Only group results are reported.

Territories were 72–100% forested, and terrain varied from flat to moderately steep (≤70%) slopes between 948–1,517 m elevation. Coniferous types (upland spruce, pine, lowland spruce) were 38.3–90.1% (59.7 ± 14.9; $\bar{x}$ ± SE) of each territory. Mature (range 12.7–68.1%; 39.4 ± 16.3)

and pole (range 14.3–67.1%; 32.9 ± 16.1) were the most abundant seral stages (Table 2.1). The young seral stage consisted entirely of forest regenerated after logging.

Pileated woodpeckers used all seral stages and forest types in both summer and winter (Fig. 2.1). Confidence interval analyses showed that the most abundant types (mixed and upland spruce) and seral stages (pole and mature) received greater use than expected compared to available habitat. The non-forest type and young seral stage were used less than available habitat. Summer use was greater than available habitat for all forest types in the pole and mature seral stages except lowland spruce (Fig. 2.2). In winter, use was greater than or equal to available for upland spruce, lowland spruce, and mixed in pole and mature seral stages, old mixed, and pole and old deciduous. Nesting season habitat use was not different from non-nesting habitat use.

Nesting season territories had more deciduous, mixed, and non-forest types, and the mature seral stage, and less coniferous type and young and old seral stages then annual territories. Within the nesting season territories, forest types and seral stages were used in proportion to available amounts. Elevations <1,100 m, which reflected the distribution of trembling aspen, were used more than available throughout the year. The slope and aspect of used habitat was in proportion to available habitat.

At the stand scale all stands received use in approximate proportion to available, with little seasonal variation. Stands 51–125 years old, 18–23 m tall, and 26–70% canopy closure were used more than available. Short (≤5 m), young (≤50 years), and late-mature (125–150 years) stands were used less than available. Stands with trembling aspen and white spruce were used more than available, and stands with all other species were used less than available.

Habitat Selection at the Foraging Substrate and Position Scales

Pileated woodpeckers foraged on wood substrates (>99.9% of foraging time) and anthills (<0.1%, n = 82 minutes). Wood substrates were dead trees (snags, stubs, stumps; 46.0%), live trees (37.8%), and logs (16.2%). Foraging methods were not different between years ($P < 0.01$) but changed between seasons (Fig. 2.3). In winter, (November–February) foraging (n = 20,676 minutes) was 94.1% excavating, including 88.3% excavating into hard substrates. Summer (April–September) foraging (n = 14,893 minutes) was 66.8% excavating, including 32.4% into hard substrates, and surface foraging increased to 33.4%. Spring (March) and fall (October) foraging (n = 4,561 minutes) was transitional between summer and winter patterns. In total, birds foraged 83.7% of the time on substrates containing carpenter ants, 8.2% on substrates containing other ant species, and 8.0% on substrates with no visible food items (Fig. 2.3). Substrates with carpenter ants were used for 90.6% of winter foraging time, and 62.5% of summer foraging time. Carpenter ants were observed in all substrate types and sizes except some soft stubs, logs, and stumps that pileated woodpeckers foraged on only in summer.

Substrate use by tree species, type, and decay class changed seasonally (Fig. 2.4). Winter foraging was mainly on coniferous species (79.6%), live trees and snags (84.3%), and hard decay class substrates (86.9%). In summer, there was increased use of deciduous species (44.7%), stubs, logs, and stumps (47.7%), and soft decay classes (49.0%). There were no seasonal differences in substrate size by species or type, but mean dbh of species ($F_{0.05, 5, 3679}$ = 50.2) and types ($F_{0.05, 4, 3679}$ = 125.9) was different. Black spruce substrate mean dbh (21.7 cm) was < all other species ($\bar{x}$ = 29.0 cm, range 27.5–32.1); and mean dbh of logs (21.8 cm) was < snags (27.4 cm) < stumps (30.7 cm), live trees (31.1 cm), and stubs (31.2 cm; Tukey's HSD, Ps < 0.001).

White spruce was used more than available in winter and less than available in summer; trembling aspen was used less than available except in spring; and balsam poplar was used more than available in summer (Fig. 2.5). There were no clear use patterns for lodgepole pine and black spruce. Dead substrates were used greater than available and live substrates less than available. Snags were used greater than available throughout the year; injured live trees were used greater than available in winter; stubs and logs were used greater than available in summer, and logs were used less than available in winter (Fig. 2.6). Substrates as small as 7.4 cm dbh were used for foraging, but pileated woodpeckers selected for larger substrates (Fig. 2.7). Substrates <20 cm dbh were used less than available, and substrates from 25–50 cm dbh were

used greater than available.

Pileated woodpeckers foraged mainly at the base of substrates (Fig. 2.8). Foraging on substrate bases or roots was 94.8% in winter and declined to 53.7% in summer. Foraging on trunks increased from 5.0% in winter to 37.3% in summer. Foraging on tops or branches occurred mainly in summer.

Cavity Tree Selection at the Territory and Stand Scales

I located 611 cavity trees from 1993–98. Trees were found in all forest types and seral stages. Within territories, trees ($n = 339$) were found in the deciduous and mixed types and the pole and mature stages more than expected and in all other types and stages less than expected (Fig. 2.9). There were no trees in the non-forest type within pair territories. Trees were found at all elevations, but <1,150 m more than expected. The slope and aspect of stands with cavity trees was in proportion to available habitat.

All stand categories received some use. Cavity tree stands had more trembling aspen than available stands. White spruce and balsam poplar occurred in proportion to available, and all other species occurred less than available. Stands with 26–70% canopy closure were used more than available, and all others were used less than available. Stands 76–100 and 151–175 years old and 18–25 m tall were used more than available, and all other classes were used in proportion to or less than available.

Cavity Tree Use and Selection at the Site, Tree, and Position Scales

Cavity tree plots had higher mean dbh and higher basal area than random plots, but they had fewer trees and conifers, and they were more open (Table 2.2). Cavity tree plots also had more large trees, large deciduous trees, and large trees with decay indicators than random plots.

Pileated woodpeckers excavated cavities in the trunks of large (dbh $\bar{x} = 45.1$, $n = 611$) trees (Table 2.3). The smallest tree was 25.8 cm, but most trees (98.9%) were >29 cm. Trees ≤35 cm were used less than available, and trees >35 cm were used greater than available in all size classes (Fig. 2.10). Balsam poplar and white spruce were larger than trembling aspen and lodgepole pine ($F_{3,605} = 25.6$, $P < 0.001$; Tukey's HSD: $P < 0.05$).The mean dbh of living and dead trees did not differ ($t = 0.09$, $P = 0.464$).

Of the 4 cavity tree species, trembling aspen was used most often (91.9%; $n = 562$). Cavities were found in both living and dead deciduous trees, but coniferous species were used only when dead. Most trees (77.3%; $n = 472$) were living, and 71.2% of dead trees ($n = 139$) were stubs. Considering only prospective trees large enough to be a cavity tree (>29 cm dbh, >7 m height), pileated woodpeckers selected trembling aspen at all scales, and used all conifer species less than available at all scales (Table 2.4). Balsam poplar was used less than available at the territory and stand scales and in proportion to available at the site scale.

When first found, 77.3% of cavity trees were living, and 92.5% were probably alive when first used by pileated woodpeckers as cavity trees (edges grown in or removed after initial excavation on at least 1 cavity/tree). Considering state when found, living trees were used less than available, snags were used in proportion to available, and stubs were used greater than available. Considering probable state when first used, living trees and snags were used in proportion to available, and stubs were used greater than available. Decay was present in all cavity trees, and 93.1% had external decay indicators (Table 2.3). Living trees had more decay indicators than available trees, and dead trees were more likely to be stubs and were harder and had less bark than available trees (Table 2.5).

Most cavities (97.1%, $n = 903$) were excavated in the trunk below the tree crown. Entrances were 2.8–20.0 m above ground, usually in a branch-free area. The lowest (2–4 m) and highest (12–20 m) height classes were used less than available, the 10–12 m height class was used in proportion to available, and height classes from 4–10 m were used greater than available. Entrances ($n = 520$) were closer to the nearest decay indicator than random points ($n = 492$; $P < 0.001$), and the distribution of entrance heights approximated the distribution of decay indicator heights (Fig 2.11). Entrances mostly (95.9%) faced a stand opening, and they were oriented SE, S, and SW greater than expected, and oriented to other directions less than expected.

DISCUSSION

Habitat Use and Selection

I found low but significant selection for older forests. In western Oregon, pileated woodpeckers used all forest types and age classes >40 years old more than expected, with strongest selection for coniferous forest 71–200 years old and mixed forest 71–100 years old, and lower than expected use of forest <40 years old (Mellen 1987). In northeastern Oregon, old growth (>8 trees ≥51 cm dbh/ha), grand fir, and stands >60% canopy closure were selected, and all other types, seral stages, and canopy closure classes were used less than expected (Bull and Holthausen 1993). Low use of young forest, including recently logged areas, was also consistent with results reported elsewhere (Conner and Crawford 1974, McClelland 1977, Mellen 1987, Chambers et al. 1997, Hutto and Young 1999). Young forest and open habitats may be used less because foraging substrates are absent or reduced, although food resources such as carpenter ants and other wood-dwelling ants may actually be more abundant in recently logged areas (Kidd and Longair 1997, Rolstad et al. 1998). Low use of these areas may also be related to the need to escape predators. Pileated woodpeckers avoid avian predators by flying to a tree and dodging around the trunk (Lima 1993). In this study, they foraged on and near (up to approximately 50 m from a tree or stand edge) isolated trees in recently logged and non-forested areas. However, they did not use completely open areas (eg recent clearcuts with no residual trees) even if foraging substrates (logs and stumps) were available.

My results support findings that excavating into wood xylem is the primary foraging method used by pileated woodpeckers (Conner 1981, Bull et al. 1986, Morrison et al. 1987, Bull and Holthausen 1993), and that carpenter ants are the principal prey (Beal 1911; Hoyt 1950, 1957; Beckwith and Bull 1985; Bull et al. 1992b). Pileated woodpeckers in my study area also made seasonal changes in foraging strategies (Hoyt 1957, Conner 1981, Bull et al. 1992b). Winter foraging was mostly (90.6%) into hard substrates containing carpenter ant colonies. In summer, carpenter ant substrates continued to be the main foraging substrate (62.5%), but there was increased use (23.8%) of soft substrates containing other ant species (Conner 1981, Bull et al. 1986). Pileated woodpeckers obtained carpenter ants and other food items in summer by surface gleaning at winter excavations and excavating in soft wood substrates, which takes less effort than excavating in hard wood.

Habitat selection was strongest at the foraging substrate scale. Use was closely related to food availability, especially that of carpenter ants. Throughout the year, pileated woodpeckers selected for snags and large diameter substrates, and against healthy live trees. Injured or partly dead live trees were selected in winter, and stubs and logs were selected in summer. There were strong seasonal selection patterns for tree species and decay class of dead substrates. Other studies also found selection for specific tree species, and for substrate type, diameter, height, and decay characteristics (Conner 1980, Bull et al. 1986, Bull and Holthausen 1993, Flemming et al. 1999). Reported differences in foraging substrate selection likely reflect variation in types and availability of substrates selected by carpenter ants and other prey species.

Carpenter ant colonies spend the winter in large diameter, hard substrates, especially near the base of standing live and dead trees (Sanders 1964, 1970). In this study, pileated woodpeckers located trees containing carpenter ant colonies during the summer and fall, and returned repeatedly to them over the winter to access a known and dependable food source. Once located, carpenter ant colonies were often foraged on repeatedly over a period of several years. Pileated woodpeckers also take advantage of bark beetle epidemics (Bull et al. 1986) but they are adapted to locating and accessing carpenter ants as their primary winter food. Their need for a dependable winter food resource means that they must first locate it and then defend it from other pileated woodpeckers, which are the only competitors capable of accessing carpenter ant colonies in winter. Defence of known food resources and cavity trees could partly explain why pileated woodpeckers defend their territory in winter. In the nesting season, pileated woodpeckers used a smaller area than their post-nesting and winter territories. Although I did not estimate prey abundance, my observations indicated that wood-dwelling ants were abundant and accessible during the nesting season. This suggests that food availability during the breeding season was

not limiting, and that the reason pileated woodpeckers establish and defend large territories in Alberta foothills forests (Chapter 3) is to secure winter food resources (McClelland 1979), which I believe were probably a limiting factor in my study area.

I observed selection at the territory and stand scales consistent with the view that pileated woodpeckers are primarily associated with mature/old forest (Conner 1980, Bull and Holthausen 1993, McClelland and McClelland 1999). However, I also documented substantial use of all available habitat categories, which indicates that pileated woodpeckers are not mature-forest obligates and further that they are flexible in habitat use and selection at the territory and stand scales (Hoyt 1957, Mellen et al. 1992, Rolstad et al. 1998). Pileated woodpeckers selected habitats that had the most preferred foraging substrates, but they exploited foraging substrates wherever they were available, irrespective of surrounding habitat. The exception to this was avoidance of open habitats with no standing trees that could be used to escape predators (Lima, 1993). I conclude that habitat selection at the territory and stand scales was primarily a function of foraging substrate availability and secondarily a function of predator avoidance.

Selection was identified at all scales but was most significant at the foraging substrate scale. Pileated woodpeckers foraged on substrates containing accessible wood-dwelling ants and other arthropods. In general these were large wood substrates that were not healthy living trees. Large substrates were probably selected because carpenter ants and other prey items were more abundant in large substrates (Sanders 1964, 1970; Bull et al. 1986; Renken and Wiggers 1989). In winter, pileated woodpeckers foraged at the base of injured living trees and hard snags and stubs. In summer, the breadth of substrates used expanded to include soft stubs, logs, and stumps, and living trees with injured or dead tops. Living balsam poplar was selected for summer surface foraging. This species has deeply furrowed and often loose bark and frequent dead tops, which may be associated with increased arthropod abundance (Jackson 1979, Conner et al. 1994).

Cavity Trees

Cavity trees were found more than expected in tall, medium-density, mixed and deciduous stands at low elevations. Other studies also found most trees in closed canopy forests with more potential cavity trees and higher basal area than available habitat (Conner et al. 1975, Bull 1987, McClelland 1977, Bull et al. 1992a, Bull and Holthausen 1993). Cavity trees were found in all forest and stand types, including open areas, indicating that pileated woodpeckers showed considerable flexibility in cavity tree selection at the territory and stand scales. Cavity trees located in young, open, stands have been previously reported (Conner 1973, McClelland 1977, Millar 1992, Naylor et al. 1997). Use of these habitats, including young forest and urban areas with large remnant trees (Bull 1987, Bull and Jackson 1995), indicates that availability of potential cavity trees is probably the most important selection factor at the territory and stand scales (Kirk and Naylor 1996).

Within stands, pileated woodpeckers selected sites with high basal area and more potential cavity trees, but there were fewer trees overall and cavity tree sites were more open than random sites. Selection for more potential cavity trees is consistent with previous reports (Bull 1987), but selection for open sites has not been previously reported for pileated woodpeckers. In Sweden, the black woodpecker (*Dryocopus martius*) also preferred open sites around cavity trees, possibly because open sites were less vulnerable to predators (Rolstad et al. in review). Failed cavity-user nests in an Arizona study were more concealed by foliage and were closer to conifers than successful nests (Li and Martin 1991). Pileated woodpeckers often perched in a nearby tree in an alert position before approaching cavity trees. Potential predators such as the northern goshawk (*Accipiter gentilis*) and American marten (*Martes americana*) would be easier to detect when there are open areas around cavity entrances. In addition to reducing predation risk, nest trees in open areas may also reduce competition for cavities (Short 1979).

Pileated woodpeckers excavate cavities in large trees, often the largest available (Conner et al. 1975, McClelland 1979, Peck and James 1983, Bull 1987). Large trees are less likely to break at the cavity location (Harris 1983, Harestad and Keisker 1989), and they are more likely to have stem decay (Basham 1958, Hiratsuka et al. 1990). Cavity tree size in this study was comparable to that of similar forest regions (Campbell et al. 1990, Harestad and Keisker 1989, Millar 1992),

and there was positive selection for trees >35 cm dbh. Pileated woodpeckers can excavate in solid wood (Bull 1987), but prefer to excavate cavities in trees partially softened by fungal decay (Conner et al. 1976, Harris 1983, DeGraaf and Shigo 1985, McClelland and McClelland 1999). They select live trees or hard snags with heartwood decay but relatively sound sapwood (McClelland and McClelland 1999), which provides protection from predators such as bears (Dixon 1927, Kilham 1971, Harris 1983). All cavity trees in this study had heartwood decay.

I found strong selection for tree species, type, and external characteristics (branching, bark, and sap). Pileated woodpeckers excavate cavities in many tree species (Hoyt 1957, Bull and Jackson 1995) and relative use of live or dead trees with intact or broken tops varies geographically (Kirk and Naylor 1996). Smooth, branch-free trunks may be preferred because they facilitate pileated woodpecker movements and reduce predation risk (Bull 1987), but trees with rough bark (eg balsam poplar) are also used. Large quantities of sap released when sapwood is excavated may discourage pileated woodpeckers from excavating in living coniferous species (Saenz et al. 1998). Living and dead deciduous trees, especially trembling aspen, and dead coniferous trees provided the preferred size, decay characteristics, and external configuration in the study area. Trembling aspen was also selected in areas with similar forest composition (Wedgwood 1988, Harestad and Keisker 1989, Millar 1992) and is selected wherever it occurs (Kirk and Naylor 1996). This species is prone to stem decay caused by the false tinder fungus (*Phellinus tremulae*; Basham 1958), that produces decay columns surrounded by living sapwood that were preferred by pileated woodpeckers. Trees with visible sign of *P. tremulae* infection were abundant in the study area (28.2% of trembling aspen >35 cm dbh). Trembling aspen also has few branches on the main trunk, smooth bark, and low sap when living sapwood is excavated. Dead trees used by pileated woodpeckers, especially those with broken tops, had similar characteristics to trembling aspen.

I found no relationship between tree size and cavity height, but cavity entrances were found in the 4–10 m height classes more than expected, and they were closer to visible decay indicators than random points. Decay columns in trembling aspen infected with false tinder fungus usually start >200 cm above ground and extend 370 ± 21 ($\bar{x}$ ± SE) cm above and below conks (Hinds 1963, Hiratsuka 1990). Decay column height, diameter, and hardness were probably the main factors in cavity placement. I did not measure decay characteristics, but there was decay at all cavity locations. Inspection of wood chips and cavities suggested that most cavities were located near the top of a decay column, where the decay column diameter was large enough to support a cavity and the heartwood was still relatively hard (Miller et al. 1979, Harris 1983). Cavity locations of red-naped sapsuckers (*Sphyrapicus nuchalis*) nesting in trembling aspen were also related to decay column diameter and height (Daly 1993). Similar to the findings of others, all recently excavated cavities had living or hard dead sapwood at the cavity entrance and most cavities were in branch-free areas with no bark or smooth bark (McClelland 1977, Bull 1987). Cavity entrances faced 135–225 degrees more than expected. Bull (1987) had similar results, and thought that entrance orientation was related to tree lean. Lean did not appear to have importance in my study area because most of the cavity trees had little lean. I believe that entrance orientation was primarily related to the position of the cavity tree in relation to nearby stand openings. Entrances usually faced these openings, which facilitates adult access to the cavity and may reduce predation risk. However, this observation does not explain the tendency for entrances to face 135–225 degrees. Entrances facing towards the sun and away from prevailing winds may provide advantages to pileated woodpeckers in the study area.

Pileated woodpeckers used most available habitat for foraging and other activities, including cavity tree use, at all scales examined. The magnitude of selection generally increased from larger scales (territory, stand) to smaller scales (foraging substrate or cavity tree, position), indicating that habitat use and selection was primarily related to the substrate and position scales. Large foraging substrates containing carpenter ants and cavity trees with stem decay were selected and small substrates and healthy trees were avoided. Pileated woodpeckers appear to depend on large substrates with damaged or decayed portions and not on stand or territory composition. They showed considerable flexibility in meeting their habitat needs at larger scales, and selection at these scales was likely a function of the availability of habitat at the substrate scale, and possibly on presence of trees for predator avoidance.

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Table 2.1. Forest type and seral stage composition (proportion) of 14 pileated woodpecker pair territories at Hinton, Alberta, 1993–96.

	Territory number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Pooled[b]
Forest type[a]	Proportion of habitat in territory														
Non-forest	4.1	2.6	5.5	16.4	5.5	10.9	4.1	2.4	4.3	14.4	28.3	18.0	2.7	0.4	8.4
Deciduous	11.5	1.8	16.4	8.0	10.3	6.1	2.5	16.0	6.3	34.5	3.6	2.2	21.0	3.3	11.7
Mixed	31.2	29.9	6.0	36.0	23.3	19.5	3.3	15.9	25.0	7.9	29.7	41.0	13.4	27.2	20.3
Upland spruce	15.2	43.7	14.4	27.1	45.6	54.6	8.4	36.7	24.5	3.0	31.0	27.9	9.1	55.8	25.4
Lowland spruce	37.7	22.0	2.4	12.0	9.6	6.3	2.6	26.1	34.6	7.6	6.1	9.6	3.7	8.1	13.4
Pine	0.2	0.0	55.2	0.5	5.8	2.6	79.1	2.9	5.3	32.6	1.2	1.4	50.2	5.1	20.9

	Territory number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Pooled
Seral stage	Proportion of habitat in territory														
Young	5.5	20.9	11.3	8.1	0.0	0.0	10.7	1.9	3.9	0.0	0.6	0.0	33.5	0.0	9.1
Pole	27.7	20.4	67.1	29.3	19.7	37.5	48.9	54.4	25.0	14.3	40.0	50.5	21.9	18.3	32.9
Mature	57.7	42.2	12.7	26.2	65.8	26.4	33.1	37.0	27.7	68.1	28.5	29.5	37.3	51.6	39.4
Old	9.0	16.5	8.8	36.4	14.6	36.1	7.3	6.7	43.4	17.5	30.9	19.9	7.3	30.1	18.5

[a] See methods section for definitions of forest types and seral stages.

[b] Pooled values are derived from the sum of the area in each type or seral stage for all territories combined.

Table 2.2. Comparison of pileated woodpecker cavity tree plots with random plots located in the same stand at Hinton, Alberta, 1993–98.

	Cavity tree plots		Random plots		
Variable[a]	$\bar{x}$	SE	$\bar{x}$	SE	P-value
Density trees >29 cm dbh	7.8	4.3	6.0	4.2	<0.001
Density deciduous trees >29 cm dbh	6.4	4.3	4.1	3.9	<0.001
Density all trees	22.8	11.4	27.9	12.2	<0.001
Average dbh (cm)	27.3	6.6	23.4	5.8	<0.001
Density trees >29 cm dbh with conks	4.1	2.9	1.7	1.3	<0.001
Density trees >29 cm dbh, snag or stub >7m	0.7	1.0	0.4	0.7	<0.001
Density trees >29 cm dbh with strong decay indicators	1.4	1.3	1.1	1.4	0.077
Density trees >29 cm dbh with weak decay indicators	0.5	0.7	0.3	0.5	0.027
Density conifers	11.3	12.5	15.7	14.9	<0.001
Basal area (m^2/0.04 ha)	1.5	0.6	1.3	0.5	<0.001
Openness index[b]	23.5	8.2	17.4	8.2	<0.001

[a] All density variables refer to the number of trees/0.04 ha.

[b] Total of distance in m from cavity tree or centre tree to the 2 closest trees in each quarter of a circular 0.04 ha plot. The plot radius (11.28 m) was used if trees were missing for any of the 8 measurements.

Table 2.3. Species, diameter at breast height (dbh), life status, and decay status of pileated woodpecker cavity trees in Alberta, 1993–98.

	Total	Live trees				Dead trees					Decay indicators[a]		
			Dbh			Snag	Stub	Dbh			Conks	SDI	WDI
Tree species	*n*	*n*	Range	$\bar{x}$	SE	*n*	*n*	Range	$\bar{x}$	SE	%	%[b]	%[c]
Trembling aspen	562	456	25.8–70.6	44.4	7.3	36	70	27.6–86.0	44.3	9.7	59.4	36.3	4.3
Balsam poplar	31	16	40.7–86.7	56.5	11.0	3	12	49.5–84.1	57.8	15.0	9.7	71.0	0.0
White spruce	10					1	9	37.8–64.8	50.8	9.4	20.0	80.0	0.0
Lodgepole pine	8						8	29.6–61.8	40.6	10.9	0.0	100.0	0.0
All species	611	472	25.8–86.7	44.8	7.7	40	99	27.6–86.0	46.0	11.2	55.5	34.6	3.9

[a] Decay indicators: Conks = confirmed decay; SDI = strong decay indicators (stem crack, crook, swelling, broken top; large dead branch stubs); WDI = weak decay indicators (top dead or forked; scars; galls; animal damage).

[b] Proportion of trees without conks but with SDI.

[c] Proportion of trees without conks or SDI but with WDI.

Table 2.4. Cavity tree type and species used by pileated woodpeckers, compared to abundance at site, stand, and territory scales, at Hinton, Alberta, 1993–98.

Tree type	Tree species	Cavity trees	Available trees[a]					
			Site scale		Stand scale		Territory scale	
		n = 611	n = 2,140		n = 1,452		n = 15,330	
		Proportion	Proportion	Conclusion[b]	Proportion	Conclusion[b]	Proportion	Conclusion[b]
Live	Trembling aspen	0.746	0.705	Use > Ab	0.399	Use > Ab	0.199	Use > Ab
	Balsam poplar	0.026	0.040	Use < Ab	0.040	Use < Ab	0.040	Use < Ab
	White spruce	0.000	0.100	Use < Ab	0.118	Use < Ab	0.316	Use < Ab
	Lodgepole pine	0.000	0.050	Use < Ab	0.058	Use < Ab	0.214	Use < Ab
	Subalpine fir	0.000	0.000	Use = Ab	0.006	Use < Ab	0.028	Use < Ab
	Black spruce	0.000	0.014	Use < Ab	0.012	Use < Ab	0.143	Use < Ab
Snag	Trembling aspen	0.059	0.039	Use > Ab	0.016	Use > Ab	0.006	Use > Ab
	Balsam poplar	0.005	0.003	Use < Ab	0.005	Use = Ab	0.005	Use = Ab
	White spruce	0.002	0.007	Use < Ab	0.011	Use < Ab	0.010	Use < Ab
	Lodgepole pine	0.000	0.002	Use = Ab	0.003	Use < Ab	0.015	Use < Ab
	Subalpine fir	0.000	0.000	Use = Ab	0.000	Use = Ab	0.000	Use = Ab
	Black spruce	0.000	0.000	Use = Ab	0.003	Use < Ab	0.009	Use < Ab
Stub	Trembling aspen	0.115	0.033	Use > Ab	0.006	Use > Ab	0.004	Use > Ab
	Balsam poplar	0.020	0.000	Use > Ab	0.001	Use > Ab	0.000	Use > Ab
	White spruce	0.015	0.002	Use > Ab	0.001	Use > Ab	0.001	Use > Ab
	Lodgepole pine	0.013	0.002	Use > Ab	0.001	Use > Ab	0.009	Use > Ab
	Subalpine fir	0.000	0.000	Use = Ab	0.000	Use = Ab	0.000	Use = Ab
	Black spruce	0.000	0.001	Use = Ab	0.000	Use = Ab	0.000	Use = Ab

[a] Includes only trees >29 cm dbh and >7m height; smaller and shorter trees were rarely used by pileated woodpeckers as cavity trees.
[b] Use versus abundance comparisons, Bailey 95% confidence intervals.

Table 2.5. Characteristics of pileated woodpecker cavity trees compared to characteristics of available trees at the site and stand scales, Alberta, 1993–98.

	Cavity trees		Available trees[a]			
			Site scale		Stand scale	
	n = 472		*n* = 1594		*n* = 939	
Live deciduous trees	Proportion	Conclusion[b]	Proportion	Conclusion[b]	Proportion	Conclusion[b]
Conks	0.597	Use > Ab	0.263	Use > Ab	0.179	Use > Ab
Dead branch stubs	0.578	Use > Ab	0.232	Use > Ab	0.232	Use > Ab
Stem cracks	0.220	Use > Ab	0.095	Use > Ab	0.102	Use > Ab
Stem swelling	0.129	Use > Ab	0.022	Use > Ab	0.009	Use > Ab
Stem crook	0.083	Use > Ab	0.017	Use > Ab	0.004	Use > Ab
	n = 139		*n* =199		*n* = 101	
Dead trees	Proportion	Conclusion[b]	Proportion	Conclusion[b]	Proportion	Conclusion[b]
Intact top (snag)	0.288	Use < Ab	0.558	Use < Ab	0.802	Use < Ab
Broken top (stub)	0.712	Use > Ab	0.442	Use > Ab	0.198	Use > Ab
<50% bark	0.676	Use > Ab	0.156	Use > Ab	0.099	Use > Ab
≥50% bark	0.324	Use < Ab	0.839	Use < Ab	0.901	Use < Ab
Decay class 1–2	0.705	Use > Ab	0.467	Use > Ab	0.545	Use > Ab
Decay class 3–4	0.295	Use < Ab	0.528	Use < Ab	0.455	Use < Ab

[a] Includes only trees >29 cm dbh and >7m height; smaller and shorter trees were rarely used by pileated woodpeckers as cavity trees.

[b] Use versus abundance comparisons, Bailey 95% confidence intervals.

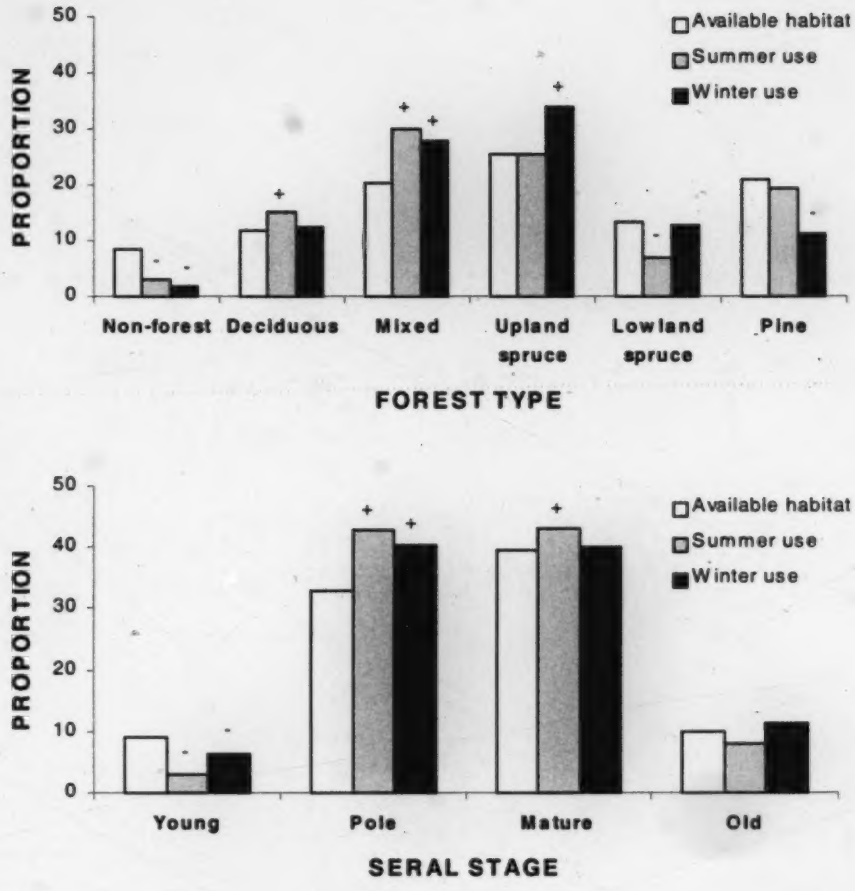

Fig. 2.1. Territory scale forest type and seral stage availability compared to pileated woodpecker use in summer and winter at Hinton, Alberta, 1993–96. The + symbol indicates use significantly greater than abundance and the – symbol indicates use significantly less than abundance, Bailey 95% confidence intervals.

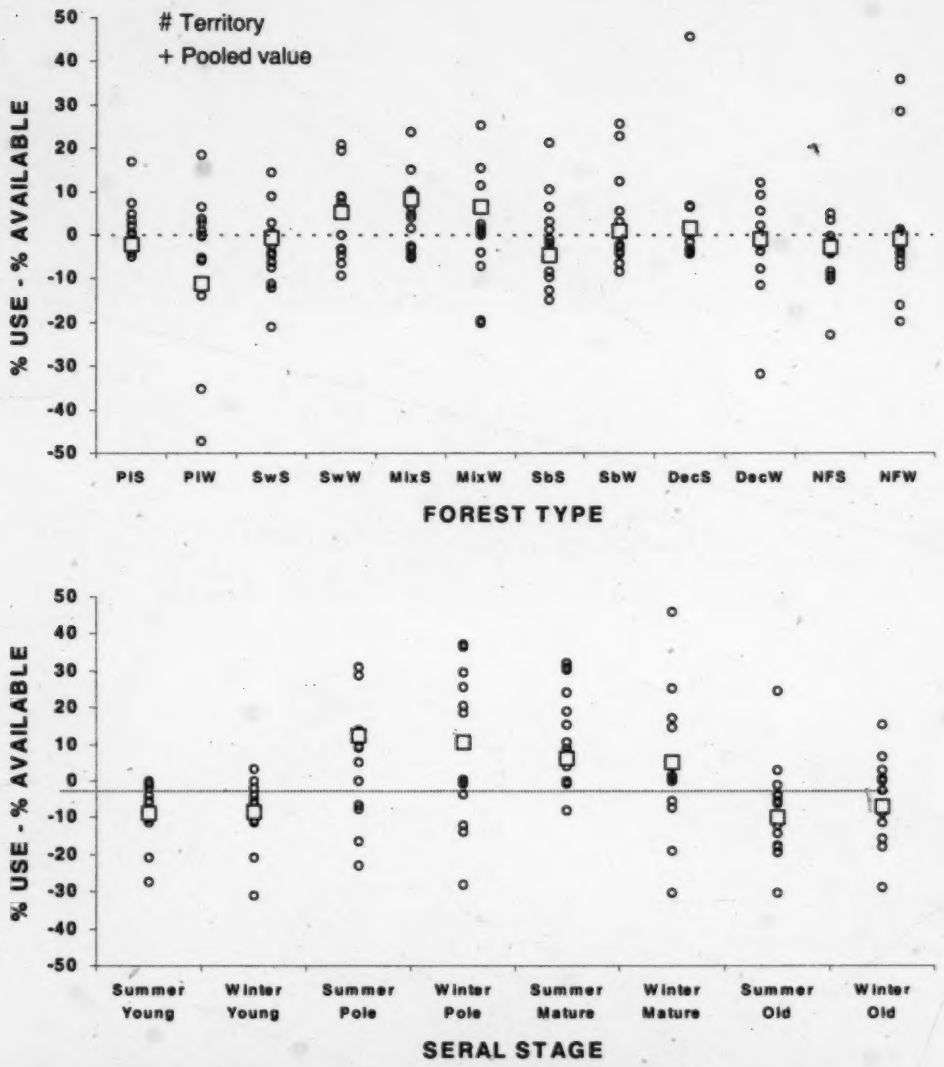

Fig. 2.2. Percent use minus % availability for forest type and seral stage within pileated woodpecker pair territories (n = 14) in summer and winter near Hinton, Alberta, 1993–96. Forest type categories are pine: summer and winter (PIS, PIW); upland spruce: summer and winter (SwS, SwW); mixed: summer and winter (MixS, MixW); lowland spruce: summer and winter (SbS, SbW); deciduous: summer and winter (DecS, DecW); and non-forest (NFS, NFW). Individual territory values are open circles and pooled values for all 14 territories are open squares.

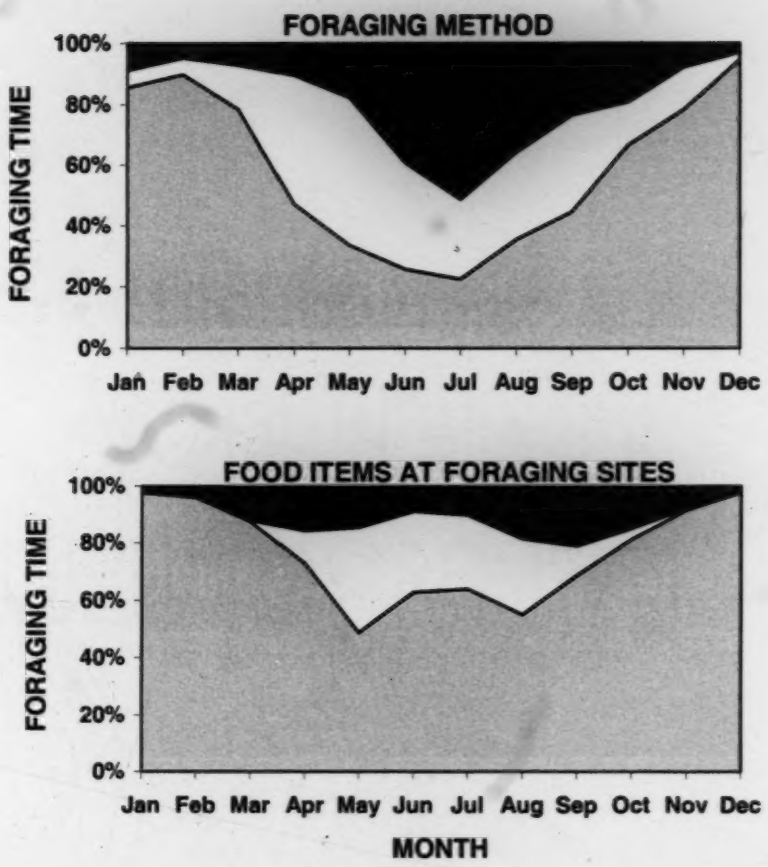

Fig. 2.3. Pileated woodpecker foraging methods and food items at foraging substrates, by month, at Hinton, Alberta, 1993–96. Foraging methods were: (1) excavation into sapwood of hard (living trees, decay classes 1–4) substrates (grey shading); (2) excavation into sapwood of soft (decay classes 5–6) substrates (white shading); and (3) surface gleaning or excavation into bark (black shading). Decay classes were: (1) recently dead, wet inner bark, sap and foliage often present; (2) dry stem and bark, fine branches present, bark present and firmly attached; (3) mostly sound stem, fine branches gone, main branches present, bark variable; (4) few or no branches, softening stem, variable bark; (5) no branches, stem soft, bark mostly gone; and (6) stem shape intact, no branches, bark gone, stem very rotten. Food items at foraging sites were: (1) carpenter ants (grey shading); (2) other ant species (white shading); and (3) no visible food (black shading).

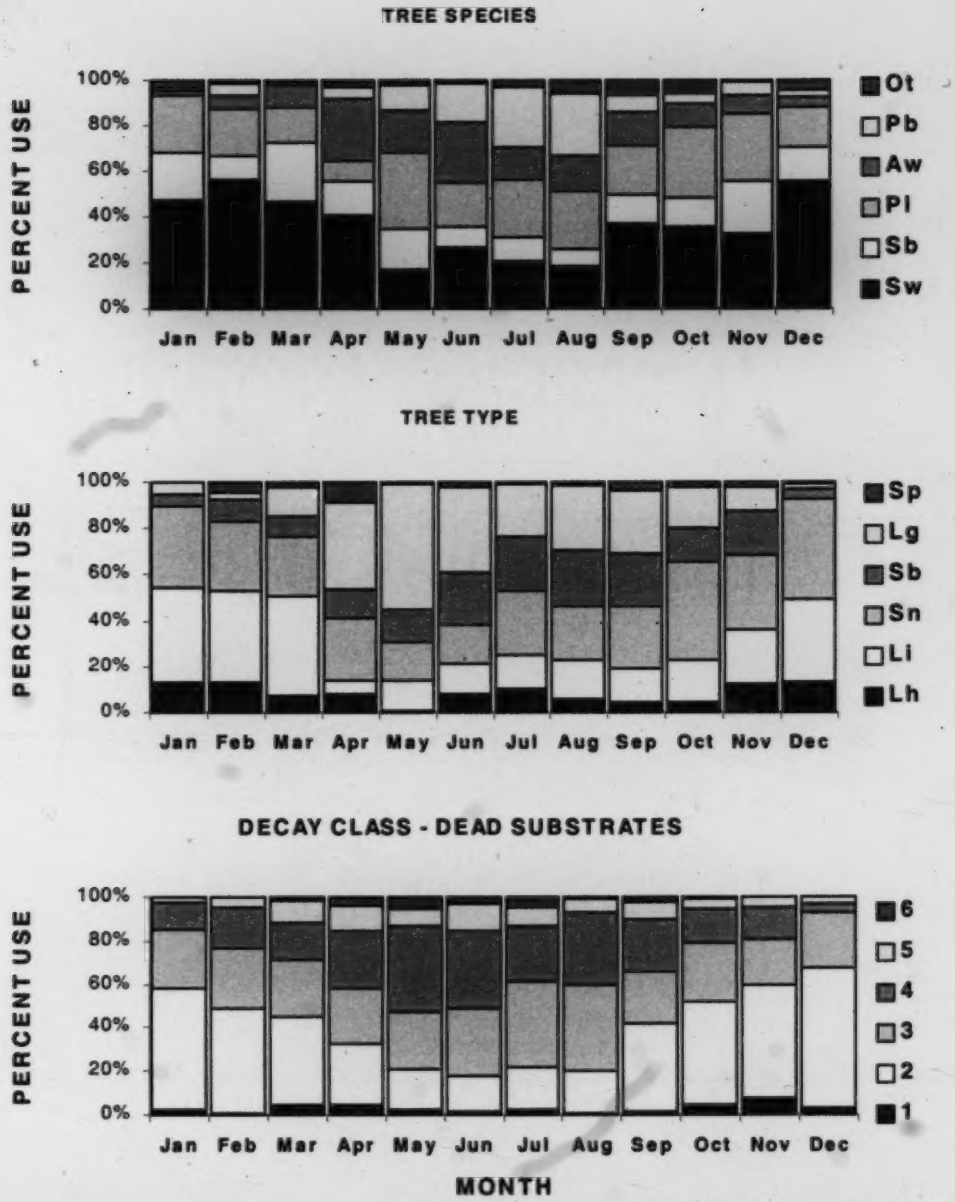

Fig. 2.4. Tree species, tree type, and decay class of foraging substrates used by pileated woodpeckers by month at Hinton, Alberta, 1993–96. Tree species were white spruce (Sw), black spruce (Sb), lodgepole pine (Pl), trembling aspen (Aw), balsam poplar (Pb), and other (Ot: subalpine fir, balsam fir, paper birch, willow, alder). Tree types were healthy live trees (Lh), injured live trees (Li), snag (Sn), stub (Sb), log (Lg), and stump (Sp). Decay classes were: (1) recently dead, wet inner bark, sap and foliage often present; (2) dry stem and bark, fine branches present, bark present and firmly attached; (3) mostly sound stem, fine branches gone, main branches present, bark variable; (4) few or no branches, softening stem, variable bark; (5) no branches, stem soft, bark mostly gone; and (6) stem shape intact, no branches, bark gone, stem very rotten

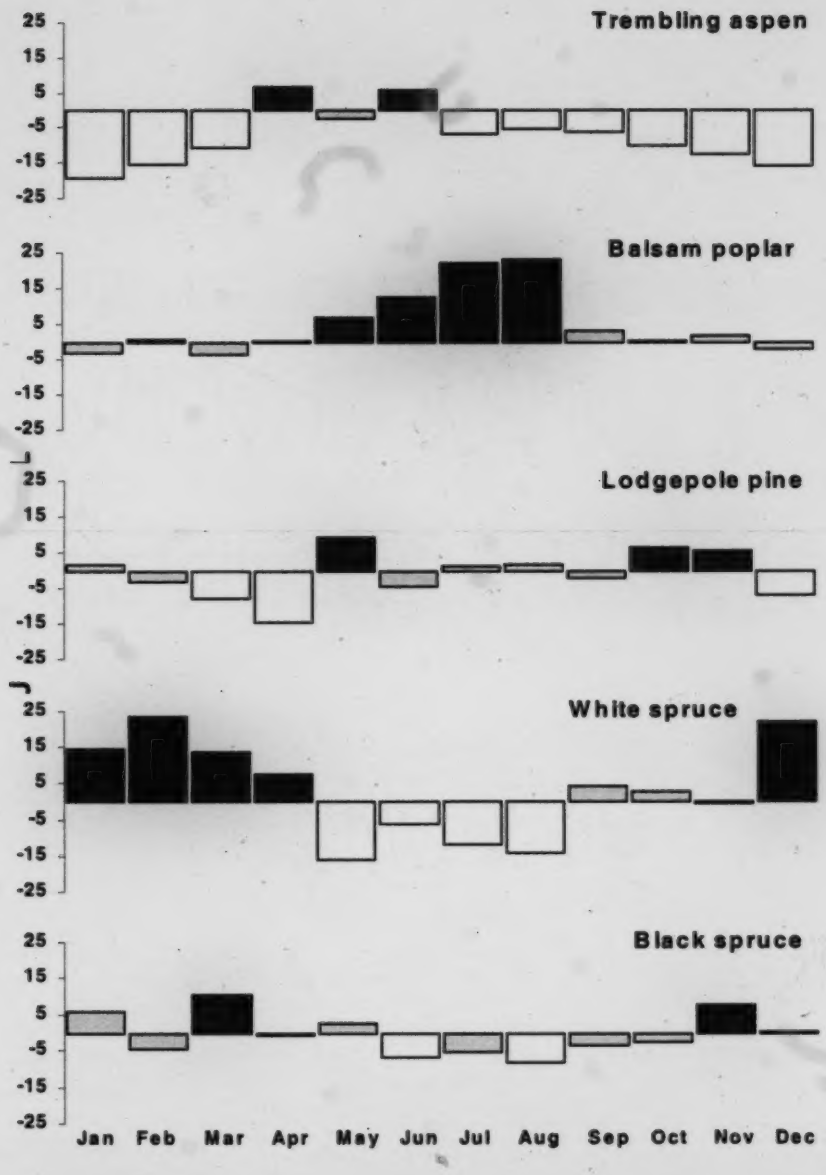

Fig. 2.5. Percent use - % available by month for major tree species used as foraging substrates by pileated woodpeckers at Hinton, Alberta, 1993–96. Black bars indicate significantly ($P < 0.05$) higher use than available, grey bars indicate not significantly different use than available, and white bars indicate significantly lower use than available.

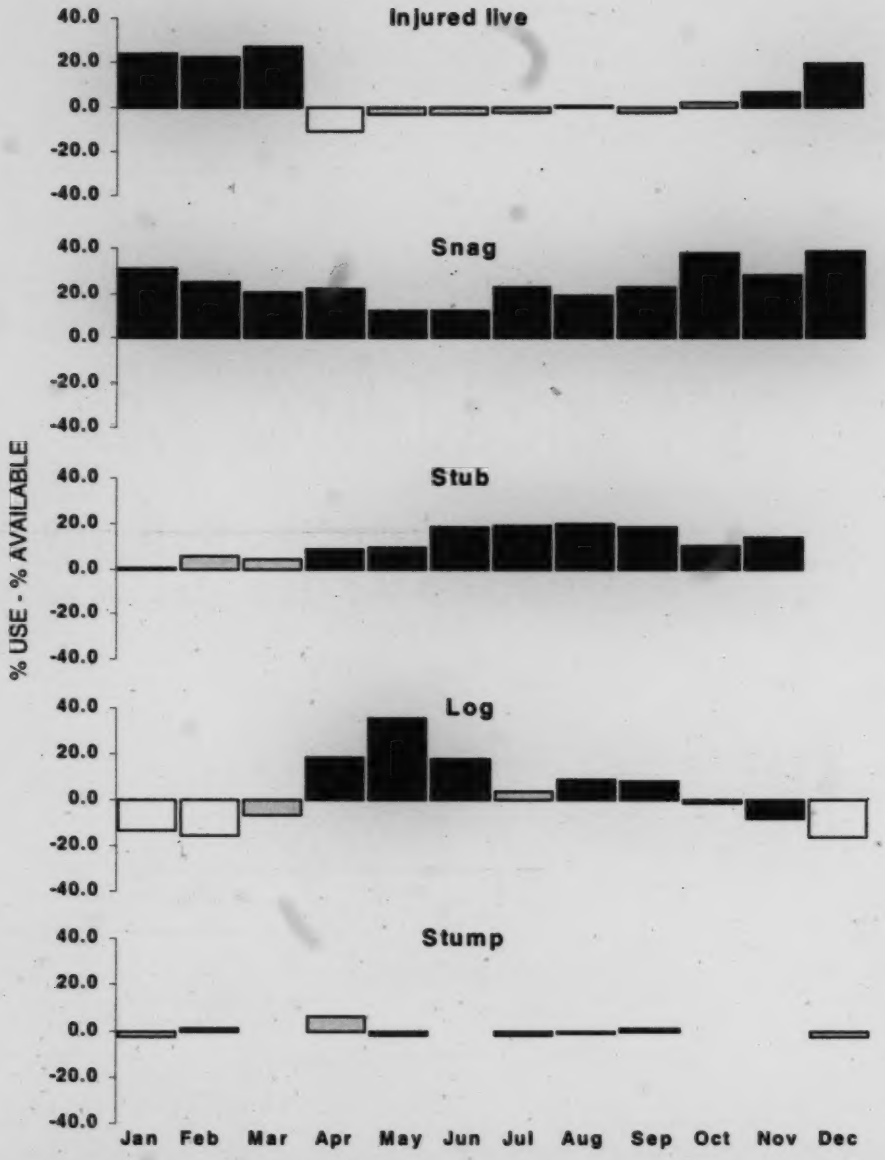

Fig. 2.6. Percent use - % available by month for type of foraging substrates used by pileated woodpeckers at Hinton, Alberta, 1993–96. Black bars indicate significantly ($P < 0.05$) higher use than available, grey bars indicate not significantly different use than available, and white bars indicate significantly lower use than available.

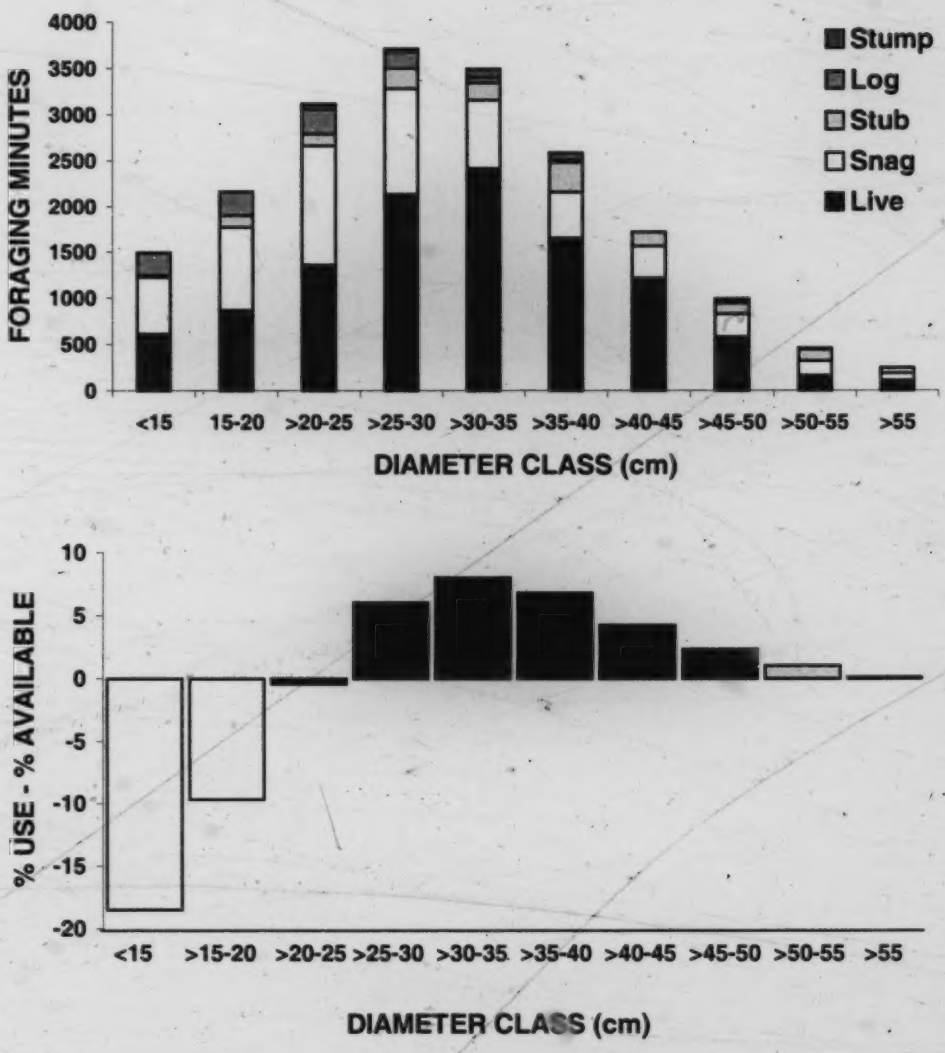

Fig. 2.7. Diameter class (cm) and % use - % available for foraging substrates used by pileated woodpeckers at Hinton, Alberta, 1993–96. For the % use figure, black bars indicate significantly ($P < 0.05$) higher use than available, grey bars indicate not significantly different use than available, and white bars indicate significantly lower use than available.

Fig. 2.8. Foraging position of pileated woodpeckers on foraging substrates at Hinton, Alberta, 1993–96.

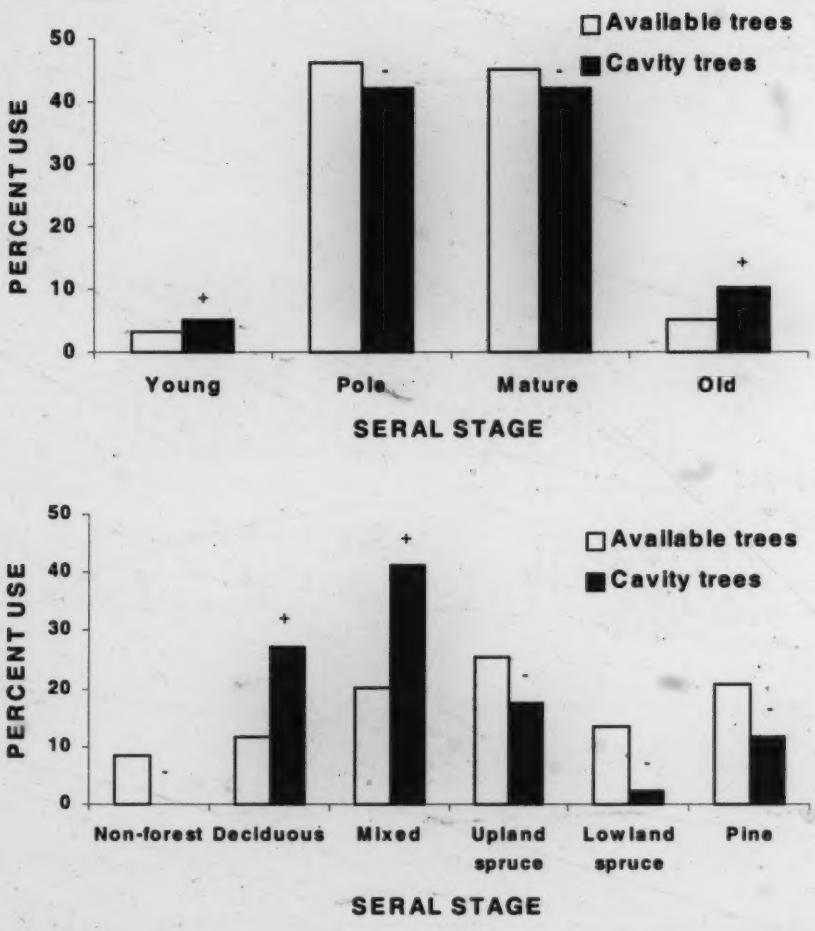

Fig. 2.9. Territory scale forest type and seral stage availability compared to location of pileated woodpecker cavity trees at Hinton, Alberta, 1993–98. The + symbol indicates use significantly greater than abundance and the – symbol indicates use significantly less than abundance, Bailey 95% confidence intervals.

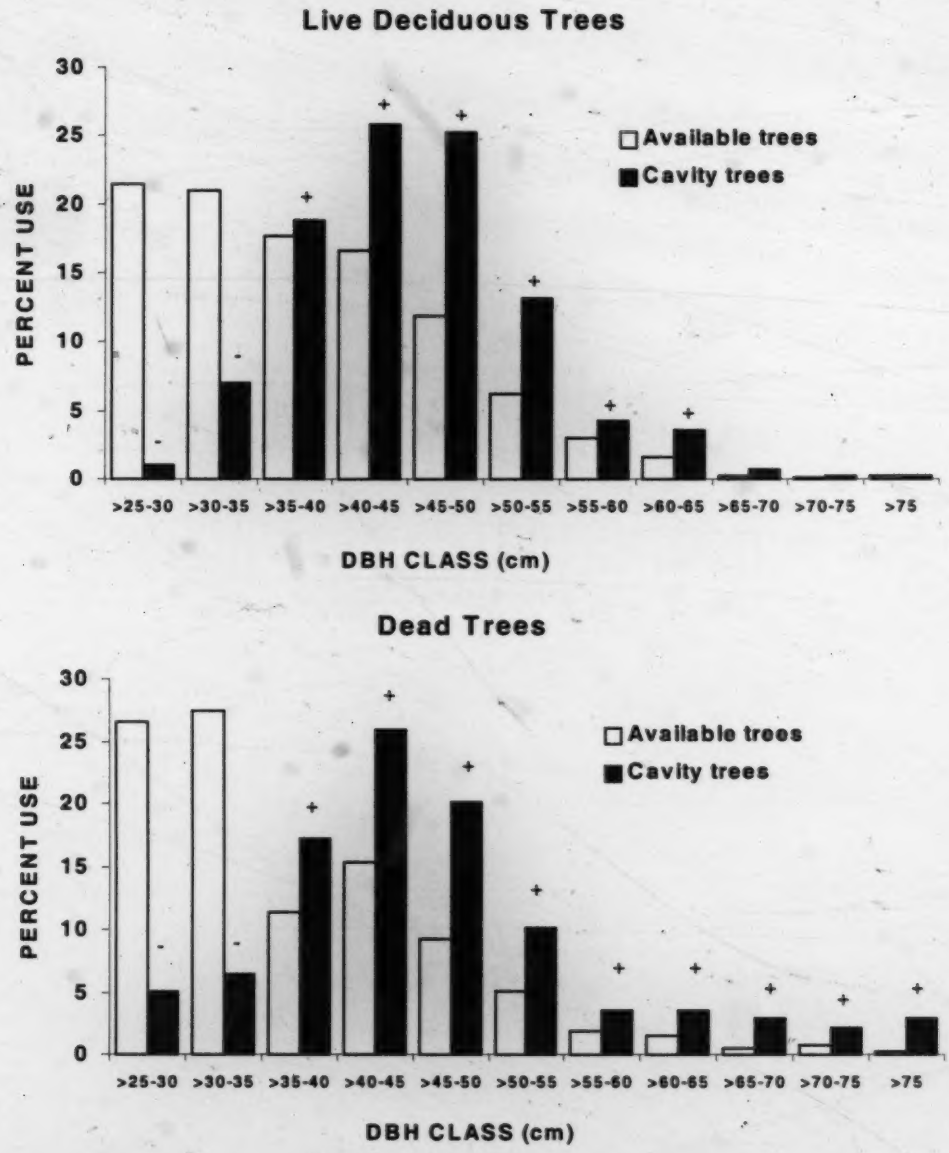

Fig. 2.10. Pileated woodpecker cavity tree size (dbh class) compared to available trees for live deciduous trees and dead trees at Hinton, Alberta, 1993–98. The + symbol indicates use significantly greater than abundance and the – symbol indicates use significantly less than abundance, Bailey 95% confidence intervals.

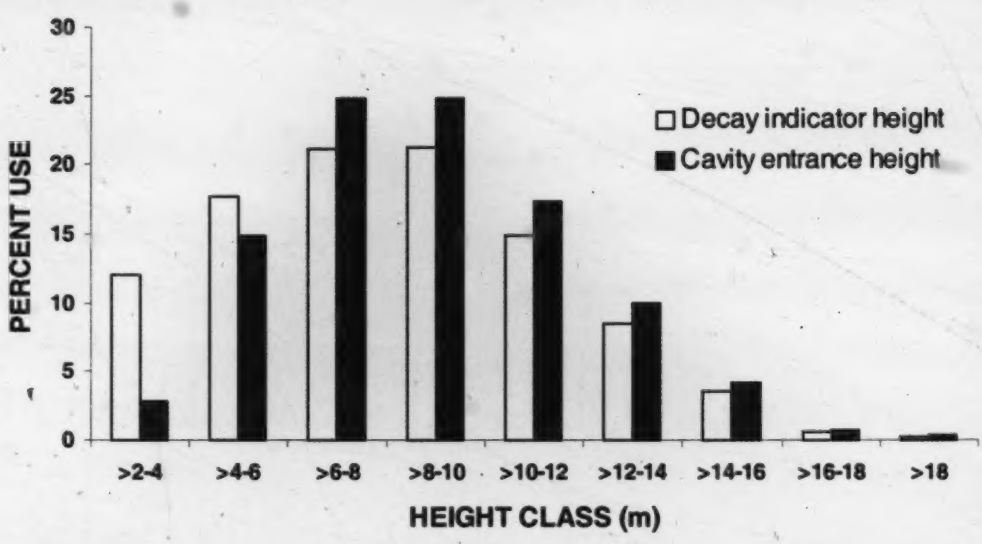

Fig. 2.11. Distribution of pileated woodpecker cavity entrance heights compared to distribution of decay indicator heights at Hinton, Alberta, 1993–98.

3. HABITAT CHARACTERISTICS RELATED TO PILEATED WOODPECKER TERRITORY SIZE, PRODUCTIVITY, AND SURVIVAL

The pileated woodpecker is a widely distributed but uncommon resident species in Alberta boreal and cordilleran forests (Semenchuk 1992). Pileated woodpeckers are most strongly associated with mature and old forests (McClelland 1977, Bull 1987, Renken and Wiggers 1989, Bull and Holthausen 1993), but they also occur in young and fragmented forests (Aubry and Raley 1992, Mellen et al. 1992). Many management agencies in Canada and the United States recognize the pileated woodpecker as a species of concern (Bonar et al. 1990, Bull and Holthausen 1993, Naylor et al. 1996, Flemming et al. 1999, Kuhnke and Watkins 1999). In part, this is due to perceived impacts of forest management practices on habitat quantity and quality. Habitat loss is the biggest issue, but pileated woodpeckers may also be sensitive to habitat fragmentation (Whitcomb et al. 1981, Rosenberg and Raphael 1986, Robbins et al. 1989, Bull and Jackson 1995, McClelland and McClelland 1999).

Determining the effects of forest management requires an investigation of relationships between habitat characteristics and pileated woodpecker response. If habitat loss and fragmentation are important factors, birds living in high quality habitat should have smaller territories and higher productivity and survival rates than birds living in lower quality habitat (Schoener 1968, Van Horne 1983, Morrison et al. 1992). As habitat quality declines, there may be a threshold below which habitat quality is insufficient to support a viable population of pileated woodpeckers.

Pileated woodpecker productivity, survival, and territory size have not been investigated in the Alberta foothills, which are near the northern limits of pileated woodpecker distribution. Research in Missouri and Oregon found an inverse relationship between some habitat characteristics and pileated woodpecker density or territory size (Renken and Wiggers 1989, 1993, Bull and Holthausen 1993). Pileated woodpecker productivity and survival have been described from other areas (Bull and Jackson 1995) but there have been no studies comparing habitat quality and fitness response.

I studied relationships between habitat and fitness response of pileated woodpeckers in Alberta foothills forests to evaluate the potential response of pileated woodpeckers to forest management regimes. My objectives were to describe territory size, productivity, and adult survival, to identify variables associated with high-quality habitat, and to compare habitat quality variables with bird response variables. I compared: (1) habitat quality variables and territory size; (2) habitat quality variables compared to productivity and survival, and (3) territory size compared to productivity and survival.

STUDY AREA

The study area was the 26,000-km^2 Foothills Model Forest in the Rocky Mountain and Foothills Natural Regions of west central Alberta, Canada (Beckingham et al. 1996). Productivity information was also obtained on an opportunistic basis from forested areas of central Alberta and British Columbia. This area was roughly bounded on the west by Prince George, on the north by Fort McMurray, on the south by Red Deer, and on the east by the Alberta-Saskatchewan border. Most information was obtained within 14 territories of radio-tagged pileated woodpecker pairs within approximately 50 km of Hinton, Alberta (127°46'N, 117°39'W). Forests above 1,150 m were dominated by lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmanni*). Below 1,150 m, mixed forests were co-dominated by lodgepole pine, trembling aspen (*Populus tremuloides*), white spruce (*P. glauca*), and balsam poplar (*Populus balsamifera*; Beckingham et al. 1996). Other common tree species included black spruce (*Picea mariana*) and subalpine fir (*Abies lasiocarpa*). Forest age composition was 12% young (<30 years), 30% pole (31–100 years), 52% mature (101–160 years) and 6% old (>160 years; Weldwood of Canada, unpublished data).

METHODS

Radio Telemetry

I followed 32 radiotagged adult pileated woodpeckers and 1 juvenile in 14 pair territories from June 1993–June 1996. Birds were initially captured in 1993 (n = 2), 1994 (n = 16), and 1995 (n = 15) at nest trees (n = 28) or roost trees (n = 4), using a hoop net or board trap (Bull and Pedersen 1978). Each bird was fitted with an 11-g, 2-stage transmitter with a mortality sensor attached with a backpack harness. Birds were recaptured to replace transmitters when batteries failed at 5–12 months. I radiotagged both pair members in 12 territories, and 1 bird in 2 territories. When birds died, I radiotagged new birds that replaced them. Birds were followed for 3 years in 2 territories, 2 years in 12 territories, and 1 year in 2 territories. Individuals were followed over periods of 9–763 days (n = 6,120 locations, range 6–488 locations/bird). Transmitters were removed in June 1996 from all birds except 3 that could not be recaptured because their transmitter batteries had failed.

Territory Size

I calculated minimum convex polygon (MCP; Mohr 1947) size in ha for each bird and pair territory, which included the combined locations for both members of a mated pair. Sample size, independence of observations, and treatments of outlier points are important considerations when using the MCP method. I used all data points except for 19 locations for 2 birds that temporarily left their territory after their respective mates died. Two MCP areas added together were used for a female that left her territory for an extended period after her mate died, but later returned and successfully nested in the original territory. Pileated woodpeckers were highly mobile and could fly to any portion of their territory within a few minutes. Typical daily patterns of habitat use were of 2 types: (1) birds flew to and then concentrated use in a small area of their territory before moving to another area; and (2) birds moved frequently and used large portions of their territory. This resulted in daily follow locations that were either clustered or dispersed. To examine spatial and temporal autocorrelation effects, I plotted MCP area against cumulative location number. For annual territory size, an MCP area asymptote occurred at 30–50 locations when locations were collected on ≥10 days over periods of ≥90 days. Therefore, I determined MCP for all $n \geq 50$ that met these criteria for 2 periods: (1) annual = 1 June–31 May; and (2) cumulative = entire monitoring period. I also calculated territory size for the nesting period, which was defined as the period when eggs or young were in nests (1 May–30 June) in each year. As adults were very mobile during this period, I used all $n \geq 20$ collected on ≥3 days for this calculation.

Productivity

I determined clutch size by climbing nest trees and inspecting nest cavities using a small flashlight and mirror. Cavities were inspected again if there was doubt after the first inspection about whether or not a full clutch had been completed. As most nests were found after eggs had been laid or hatched, the number of nesting attempts that resulted in fledged young were estimated using only radio-tagged birds that were followed for successive years. The number of fledged young for each known nesting attempt was estimated by assuming that the number of young observed at nest entrances within 1 week of the expected fledging date was representative of the number of young that actually fledged. The maximum number of young observed inside nest cavities before they were old enough to climb to the entrance to be fed was 3. Up to 3 young could appear at the nest entrance during the last 2 weeks before fledging. However, 2 young at the entrance at a time were more usual, so I continued observations at entrances over multiple appearances and used the sex of young to determine if there were more than 2. Using this method, some nests with 3 young of the same sex may have been classified as having only 2 young. This possibility occurred for 8 of 104 nests, so the reported number of fledged young should be considered as a minimum estimate. Nests that produced ≥1 fledged young were considered successful.

Mortality and Survival

I retrieved transmitters emitting mortality pulse rates as soon as they were detected and used site and carcass indicators to determine mortality causes. Raptor predation was indicated by carcasses in raptor nests, raptors flushed from carcasses with talon puncture wounds, plucked carcasses, piles of plucked feathers, bones or skeletons with flesh torn from bones, raptor droppings/feathers, and snow sign. Mammal predation was indicated by tooth marks on carcasses, bones, and transmitter packages, chewed feathers, mammal droppings or hair, and snow sign. Simple annual survival was calculated by dividing the number of birds alive at the end of each reproductive year (June 1) by the number of birds radio-tagged during the period. I also calculated survival as a rate using the staggered-entry Kaplan-Meier method (Kaplan and Meier 1958, Pollock et al. 1989). I calculated a mortality rate for each pair by dividing the cumulative number of weeks that birds within each territory were at risk by the number of deaths for the territory for: (1) the nesting season, using an average if there was >1 nesting season monitored for the territory; and (2) the entire monitoring period.

Habitat Quantification

For each MCP area, I analyzed digital forest cover inventory to determine percent area by forest type, seral stage, canopy closure class, height (m), age (years since stand origin), and tree species composition (classified to the closest 10%). Forest types were (1) pine = ≥50% lodgepole pine, <20% deciduous; (2) upland spruce = ≥50% white spruce or subalpine fir, <20% deciduous; (3) lowland spruce = ≥50% black spruce or tamarack, <20% deciduous; (4) deciduous = ≥80% aspen or balsam poplar; (5) mixed = ≥20% each coniferous and deciduous; and (6) non-forest = <6% forest cover (water, non-vegetated, grass, shrub, settlements). Tamarack was considered to be a coniferous species. Each type was classified into 4 seral stages based on stand age. Seral stages for coniferous types (pine, upland spruce, lowland spruce) were (1) young (<30 years); (2) pole (31–100 years); (3) mature (101–160 years); and (4) old (>160 years old). Seral stages for deciduous and mixed types were young (<30 years), pole (31-80 years), mature (81–120 years), and old (>120 years). Canopy closure classes were (1) non-forest = <6%; (2) A = 6–25%; (3) B = 26–50%; (4) C = 51–70%; and (5) D = >70%).

I used fixed-area plots to sample wood substrates, which were measured if ≥0.5 of the base was within the plot. Tree species and type (live, snag (dead tree with intact trunk), stub (dead tree with broken trunk), stump (cut with saw), log) were determined for each used wood substrate. Diameter at breast height (dbh) was measured 1.3 m above the base for trees, snags, stubs and logs ≥1.3 m, and diameter was measured at the top for stumps, stubs, and logs <1.3 m tall. Height or length to the closest 0.1 m was estimated using a clinometer or measured with a tape measure for stubs, stumps, and logs. Bark cover: (1) <25%; (2) 26–50%; (3) 51–75%; and (4) >75%), and decay class: (1) recently dead, wet inner bark, sap and foliage often present; (2) dry stem and bark, fine branches present, bark present and firmly attached; (3) mostly sound stem, fine branches gone, main branches present, bark variable; (4) few or no branches, softening stem, variable bark; (5) no branches, stem soft, bark mostly gone; and (6) stem shape intact, no branches, bark gone, stem very rotten, were estimated for dead wood types. Decay classes were grouped into hard (decay classes 1–3) and soft (classes 4–6) categories.

Presence and type of visible decay indicators were recorded for living trees. Fungal conks were considered to be conclusive decay evidence. Strong decay indicators were large dead branches or branch stubs, and trunk cracks, crooks, or swellings. Weak decay indicators were dead, forked or broken tops, and scars, galls, or injuries. Presence and position of previous pileated woodpecker excavation evidence was noted and classified as recent (within several days), fresh (within current season) or old based on the position of wood chips in relation to snow, rain, or litterfall, and wood weathering or sap extrusion at the excavation site.

For cavity tree analysis, all live trees, snags, stubs, stumps, and logs ≥10 cm diameter at the top (stumps, stubs, and logs <1.3 m height), or breast height (trees, snags, stubs, and logs ≥1.3

m) were measured in 504 0.04 ha circular plots. Half of the plots were centred on arbitrarily selected cavity trees. Each of these was paired with a plot located using a random numbers table to select repeatedly a compass bearing and distance (measured by pacing) from the cavity tree until the plot location fell within the cavity-tree stand and did not overlap with the cavity tree plot. Random plots were centred on the closest tree to the plot location. Each plot was divided into quarters using cardinal compass bearings. I calculated an openness index by measuring the distance from the cavity or centre tree to the 2 closest trees in each quarter and summing the total.

For habitat analysis, I used data for living trees and snags ≥10 cm dbh from 3,000 permanent 0.8 ha square plots systematically located in the corners of a 1.6 km^2 grid covering a 1 million ha area that encompassed the pileated woodpecker territories (Weldwood of Canada, unpublished data). From these, I randomly selected 25 plots from each forested (≥6% canopy closure) forest type for the pole, mature, and old seral stages (n = 375 plots). Data for stubs, logs, and stumps were not available from permanent sample plots, so I used data for these substrate types from 0.04 ha random plots established for cavity tree sampling (n = 74) and an additional 126 0.04 ha plots located within territories, for a total of 10 plots for each type/stage combination (n = 200). The extra plots were randomly selected from type/stage maps and located by pacing along compass bearings from reference points visible on aerial photographs. I estimated availability of substrates by multiplying proportions or means derived from the plot data for the total area sampled by forest type and seral stage times the proportion of each type/stage combination in each MCP area.

I used forest and substrate characteristics to estimate habitat quality variables. I included variables that pileated woodpeckers used significantly greater than or less than expected compared to available habitat (Chapter 2), plus several combination variables and variables to evaluate the effects of fragmentation (Table 3.1). The fragmentation variables were (1) edge index; (2) access index; and (3) fragmentation index.

I used Pearson correlation to examine relationships between variables and territory size, productivity (clutch size, nest success, and number of fledged young), and mortality (mean deaths/week). I then used multiple regression (PROC RSQUARE; SAS Institute, 1990) to compare relationships between independent habitat variables and territory size. I also compared habitat characteristics and pileated woodpecker fitness by comparing (1) habitat quality variables and (2) nesting season and cumulative territory size, to clutch size, number of fledged young, % nesting success, and mortality rate using correlation and multiple regression. Finally, I grouped the 7 smallest ($\bar{x}$ = 1,423 ha) and 7 largest ($\bar{x}$ = 2,891 ha) cumulative territories and examined differences using t - tests.

RESULTS

Territory Size

I determined 24 nesting season, 36 annual, and 29 cumulative territory areas for individual birds, and 16 nesting season, 23 annual, and 14 cumulative territory areas for pairs (Table 3.2). There were no differences (Ps > 0.256) between sexes or years for any of the comparisons. Annual territory size for pairs (range 378–3,299 ha; 1,704.4 ± 856.2, $\bar{x}$ ± SE) was not greater than annual territory size for individuals (range 299–3,185 ha; 1,360.2 ± 762.6; P = 0.056). Similarly, cumulative territory size for pairs (range 378–4,585 ha; 2,156.6 ± 1,072.8) and individuals (range 316–2,646 ha; 1,377.7 ± 970.2) was not larger than annual territory size for pairs (P = 0.065) and individuals (P = 0.467). In the nesting season, pair territory size (range 11–676 ha; 252.1 ± 173.5) was larger (P = 0.031) than individual territory size (range 11–596 ha; 186.4 ± 145.0), and the area used by the pair was considerably less than their cumulative territory area. Overlap of MCP areas for the male and female of each pair was high, but there was no overlap between adjacent territories during the nesting period and little overlap overall (Table 3.3).

Productivity

Of 158 nests found, 113 were within the Foothills Model Forest, including 62 nests within the 14 radiotelemetry territories (Table 3.4). Clutch size was 3–5 eggs (4.04 ± 0.36, $\bar{x}$ ± SE) and differed between years ($F_{4,60} = 5.80$, $P < 0.001$). Clutch size in 1998 was higher ($Q_{84,5} = 6.42$, $P < 0.001$) than clutch size from 1994–96. This may have been related to mild spring weather in 1998. Compared to long-term averages, snow melted about 4 weeks earlier, and March–May average daily temperature was 1.6°C warmer[1]. Although 95.6% of nests with known clutch sizes ($n = 69$) contained ≥4 eggs, nests inspected ≤5 days after hatching ($n = 24$) always contained ≤3 young. Adults apparently removed unhatched eggs, eggshells, and dead young from nests. Eight nests inspected on the hatching day contained 3 young, 1 egg, and shell fragments. These nests contained 3 young and no eggs, eggshells or dead young 2–4 days later. The number of fledged young per nest (Table 3.5) was 0–3 ($n = 104$ nests; 2.52 ± 0.81, $\bar{x}$ ± SE) and did not differ between years ($F_{8,95} = 1.05$, $P = 0.40$). Three (65.4%, $n = 68$) or 2 (27.9%, $n = 29$) fledged young were most common.

Nest failures ($n = 6$) occurred only after a parent died; 3 died before eggs hatched, and 3 died ≤7 days after eggs hatched. At this stage, young were probably not capable of thermoregulation and they were left exposed when the remaining adult was forced to leave them to forage. Two young fledged from each of 2 nests when an adult died ≥10 days after eggs hatched. No instances of nest predation of eggs or young were observed. Young that disappeared from nests may have died and been removed by adults, or they could have been removed by predators. Intra-specific interactions at active nests were observed between pileated woodpeckers and 3 potential nest predators (red squirrel, saw-whet owl, and boreal owl) but none involved apparent predation attempts. In each instance ($n = 5$), adult pileated woodpeckers harassed the interloper until it left the area.

All radiotagged birds attempted to nest in each year of the study. Nesting success for radiotagged pairs was 100% in 1994 ($n = 9$), 75.9% in 1995 ($n = 9$), 92.3% in 1996 ($n = 12$), and 87.1% overall ($n = 31$). Within radiotagged pair territories, 91.7% of known nests from 1993–98 ($n = 48$), were successful. In total, 93.3% of nests with known outcomes ($n = 104$) were successful.

Mortality and Survival

Seventeen radiotagged pileated woodpeckers died or disappeared: 11 were killed by raptors; 2 were killed by mammals; 1 died in an accident; and 3 had unknown fates (Table 3.6). The bird that died in an accident was roosting in a tree that split through the roost cavity and fell during a severe wind event. Birds died or disappeared in June ($n = 5$), October ($n = 1$), and winter (November–March; $n = 11$). In June, 2 carcasses were found in active northern goshawk (*Accipiter gentilis*) nests, an agitated adult northern goshawk flushed from the immediate vicinity of a freshly killed bird, a partially plucked fresh carcass was recovered from heavy cover, and a fresh skeleton (minus head, feet, and flesh) was recovered at the base of a stub at the edge of an opening. This bird was plucked elsewhere. In October a mammal killed 1 bird. In winter, birds were killed by raptors ($n = 6$) or mammals ($n = 1$). Three birds with inoperative transmitters disappeared. I believe that these birds also died, as new birds replaced all birds that died or disappeared within 1–4 months. I observed 2 instances of severed pair bonds, where 1 member of a mated pair left the territory while the other bird was still alive, so it is possible that the 3 birds that disappeared also emigrated. Northern goshawks were the confirmed or probable predator of most (81.8%; $n = 11$) birds killed by raptors. Four unsuccessful predation attempts by northern goshawks on pileated woodpeckers were observed. Northern goshawks and red-tailed hawks (*Buteo jamaicensis)* were observed in all pileated woodpecker pair territories within the study area. Other large raptor species observed or heard calling were great horned owl (*Bubo virginianus;* 8 territories), barred owl (*Strix varia;* 4 territories), and Cooper's hawk (*Accipiter cooperii;* 2 territories). Northern goshawks, great horned owls, and barred owls were the only

[1] Environment Canada weather records

large raptors in the study area during winter. Red-tailed hawks or Cooper's hawks could have killed 2 of the pileated woodpeckers that died in June.

Both birds radiotagged in June 1993 died by September. If the 3 birds with unknown fates died, annual survival was 56.3% in 1994–95 ($n = 23$), 61.9% in 1995–96 ($n = 21$), and 56.4% for both years combined (Fig. 3.1). If they did not die, survival was 68.8% in 1994-95, 66.7% in 1995-96, and 64.1% combined. There was no difference (log-rank test, $P > 0.5$) in survival by sex or between years 1994–95 and 1995–96.

Habitat and Fitness Response

Five habitat variables (% upland forest, cavity tree density, potential winter foraging substrate density, potential cavity tree density, and % stands ≥7 m tall) were negatively correlated with cumulative pair territory size (Table 3.7). Several of these variables were intercorrelated; winter foraging substrate density was positively correlated with the other 4 variables; cavity tree density was correlated to potential cavity tree density; and upland forest was not correlated to either cavity tree density or potential cavity tree density but was positively correlated to % stands ≥7m tall (Table 3.8). Percent stands ≥7 m tall was the variable best able to predict territory size ($r^2 = 0.78$, $P < 0.001$). Additional variables examined through multiple regression provided only marginal improvement to the model. Fragmentation variables were not related to territory size.

Clutch size, number of fledged young, nesting success, and adult mortality were not related ($Ps > 0.09$) to average nesting season ($r^2 = 0.02–0.06$) or cumulative ($r^2 = 0.01–0.23$) territory size. There was also no relationship ($Ps > 0.13$) between habitat quality variables and clutch size, number of fledged young, and adult mortality ($r^2 = 0.02–0.17$) using either univariate or multiple regression analysis. Pairs in the 7 smallest cumulative pair territories had larger clutches than birds in the 7 largest cumulative territories, but 7 other tests indicated no difference (Table 3.9).

DISCUSSION

Although I recorded an average of 4.2% overlap between adjacent pair territories ($n = 11$), I believe that territories of territorial pairs were usually exclusive. The MCP method does not accurately represent territorial boundaries, which were defined more accurately by birds calling and drumming while travelling along their territory boundary. Boundaries defined this way did not overlap between neighbouring pairs, and contacts between neighbouring birds always resulted in conflict and eventual retreat of the intruders if the contact was not at a territory boundary.

The average annual and cumulative pileated woodpecker individual or pair territory size was more than 4 times larger than averages determined for either pairs or individuals in previous studies (Renken and Wiggers 1989, Mellen et al. 1992, Bull and Holthausen 1993). The area used during the nesting season was within ranges previously reported, but territory size was much larger during the rest of the year. Additionally, territory sizes determined for this study must be considered as minimum estimates. Radiotagged birds sometimes could not be located within their known territories despite intensive searching (11.0% of attempted location days), but they returned to their known territory to roost at night. These birds were likely using areas outside their known territory that, if known, would have increased territory size estimates. Although I monitored radiotagged birds for longer than previous studies, territory size for individuals and pairs was relatively stable between years, so length of monitoring period does not explain the larger territory sizes in Alberta. Winters are longer and colder, with more extensive periods of snow cover, than winters in Oregon and Missouri where previous research was conducted (Renken and Wiggers 1989, Mellen et al. 1992, Bull and Holthausen 1993). Additional food resources needed because of winter severity could partially explain defence of larger territories. The forests in my study area may also have lower winter food density.

Large average territory size did not negatively affect pileated woodpecker productivity, which was higher than previously reported ranges for pileated woodpeckers. Mean clutch size in Alberta was higher than averages from other studies ($\bar{x} = 3.83$, range 1–6, Bull and Jackson 1995). The mean number of fledged young was higher than reported values of 2.0 in Montana (McClelland

1977), 2.14 in Louisiana (Tanner 1942), and 2.26 in Oregon (Bull and Meslow 1988). The number of successful nests was 93.3%. In 2 Oregon studies, 83% of nests (n = 81) were successful (Bull and Meslow 1988), and 75% of nesting pairs in good habitat fledged young (Bull and Holthausen 1993). Productivity was high and relatively consistent, which may indicate that pileated woodpecker reproduction is little influenced by habitat factors. Although sample sizes were not large, I believe the observed consistency indicates that there were probably no biologically relevant effects missed. However, I studied a relatively narrow habitat gradient, and reproduction effects may only appear at lower levels of habitat quality. Weather conditions before and during the nesting season may influence reproduction. I found evidence that clutch size was higher after a mild winter and warm spring, and reproduction was delayed in a Washington study during a cold wet spring (K. Aubry and C. Raley, personal communication).

Mean annual survival of 56.4% was comparable to other studies using birds carrying backpack transmitters. In Oregon 55% of adults followed for 2 years survived (Bull et al. 1992, Bull and Jackson 1995), and 43% of adults followed for 1 year in Washington survived (K. Aubry and C. Raley, cited in Bull and Jackson 1995). These results are lower than mean annual survival of colour-banded adults of at least 64% ± 35.40 (SD) reported in an 8-year Oregon study (Bull and Meslow 1988), so transmitters might affect survival of radiotagged birds. Predation by northern goshawks (*Accipiter gentilis*) was the major source of adult mortality. Other raptor species present in the study area that are known to kill pileated woodpeckers (Bull and Jackson 1995) were red-tailed hawk (*Buteo jamaicensis*), Cooper's hawk (*A. cooperii*), great horned owl, and barred owl (*Strix varia*). Owls are probably not major pileated woodpecker predators because owl and woodpecker activity periods have little overlap. Pileated woodpeckers are strictly diurnal, and they enter and leave roost cavities before and after main periods of owl activity. Although they often forage at ground level, mammalian predators apparently rarely kill pileated woodpeckers.

Adult survival was apparently adequate to maintain a stable population over the study period. Territory size was stable between years and reproduction was attempted in all known territories in each year of the study, with high levels of success. Non-territorial birds quickly replaced territorial adults that died.

Reported relationships between habitat characteristics and pileated woodpecker territory size and density are quite variable. In Missouri, summer territory size was inversely related to log and stump volume and canopy cover (Renken and Wiggers 1989). In Oregon, Bull and Holthausen (1993) were unable to predict territory size very well with habitat variables, but they noted that birds selected old-growth stands (>8 trees ≥51 cm dbh/ha) with ≥60% canopy closure. Pileated woodpecker density increased as mature and undisturbed forest habitat with more dead trees increased (Bull and Holthausen 1993, Renken and Wiggers 1993, Savignac 1996). However, other studies found no particular relationship between pileated woodpecker habitat use and forest characteristics. Mellen et al. (1992) did not find any relative preference for any forest type >40 years old, and Hartwig (1999) found that pileated woodpeckers showed flexibility with respect to forest age and relative abundance of residual old-growth structure. Pileated woodpeckers successfully exploit young forest landscapes that retain structures from older forests (Conner and Crawford 1974, Millar 1992, Savignac 1996, Shackelford and Conner 1997, Flemming et al. 1999).

I identified 5 variables that were inversely correlated to cumulative pair territory size. My results suggest that pileated woodpecker territory size is primarily a function of the availability of foraging substrates (food) and large trees to support nesting and roosting cavities (reproduction, shelter). Other habitat characteristics are less important, but they are often correlated with foraging substrate and cavity tree availability. However, foraging substrate and cavity tree availability is likely related to disturbance history as well as forest type and age. This could explain reported variation in habitat characteristics and pileated woodpecker response. Rolstad et al. (1998) reached a similar conclusion for black woodpeckers. They suggested that pileated woodpeckers might also depend primarily on food availability, as the two species have similar diets. If residual structures are present in young forests, pileated woodpeckers can secure sufficient resources in smaller territories. In Alberta the smallest pair territory (386 ha) was

dominated by habitat that had been logged 40 years previously, but residual trees left in logged areas were abundant.

Large territory sizes that related to lower habitat quality did not reduce fitness. I found no effect of any habitat characteristics on clutch size, fledged young, nesting success, and adult survival. I did not radiotag pairs in very low quality habitat (eg large areas of non-forest or young forest) where low habitat quality that would affect fitness response could be expected. However, I recorded successful reproduction in habitat with <10% forest cover, which suggests that pileated woodpeckers are able to maintain fitness across a wide gradient of habitat quality. In Sweden, black woodpeckers living in forest habitat fragmented by agriculture adjusted territory size to secure approximately the same amount of forest habitat as pairs living in continuous forest, with no effect on reproduction and survival (Tjernberg et al. 1993). In Norway, black woodpeckers nesting in open areas had higher nesting success than birds in denser forests, possibly because the main nest predator, the pine marten (*Martes martes*), was less abundant in open habitats (Rolstad et al. in review). Further work on pileated woodpeckers living in low quality forest habitat is needed to determine if pileated woodpeckers show similar behaviour.

Although pairs living in large territories did not have lower fitness, territory size does affect pileated woodpecker population density. Pairs defend territories year-around against other territorial pileated woodpeckers (Kilham 1979) so the main effect of lower habitat quality (increased territory size) is to reduce population density (Schoener 1968). Pileated woodpecker density may increase (reduced territory size) during periods of temporary food abundance such as bark beetle epidemics (Bull 1980). If food availability is a primary factor, territory size should change after major forest disturbances, including fire and logging. However, the short-term response of pileated woodpeckers to disturbance may not be a direct function of changes to the availability of foraging substrates unless there is a direct relationship between foraging substrate availability and the density of wood-dwelling ants, especially carpenter ants. Further work to document responses of both pileated woodpeckers and carpenter ants to disturbances would provide information to improve understanding of the effects of disturbances on pileated woodpecker territory size and stability.

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Table 3.1. Habitat variables used in correlation and regression comparison with territory size (minimum convex polygon), clutch size (eggs/nest), fledged young (number/nest), and mortality (average adult deaths/week) at Hinton, Alberta, 1993–98.

Variable name	Definition
Mean tree dbh	Mean dbh of all trees ≥10 cm dbh
% deciduous + mixed	% deciduous forest + % mixed forest
% lowland spruce	% lowland spruce forest
% upland coniferous	% spruce forest + % pine forest
% upland	% spruce + % pine + % mixed + % deciduous; ≥pole seral
% pole + mature + old	% forest ≥30 years old
% non-forest + young	% forest <30 years old or non-forest
Tree density	trees ≥10 cm dbh/ha
% forest cover	% forest >6% tree cover
Large dead tree density	Density dead trees ≥25 cm dbh/ha
Potential winter foraging substrate density	Density injured live trees + hard snags/stubs, ≥20 cm dbh/ha
Dead tree density	Dead trees (snags and stubs) >10 cm dbh/ha
Medium tree density	Trees ≥20 cm dbh/ha
Large tree density	Trees ≥25 cm dbh/ha
% trembling aspen	% trembling aspen in tree species composition of MCP territory area
% white spruce	% white spruce in tree species composition of MCP territory area
% trembling aspen + white spruce	% trembling aspen + % white spruce in tree species composition of MCP territory area
% tall stands	% stands ≥18 m height
% stands ≥7 m)	% stands ≥7 m height
Mean stand height	Mean stand height
% closed stands	% stands >25% canopy closure
Mean canopy closure	Mean stand canopy closure
% ≤50 years	% stands ≤50 years old
% >75 years	% stands >75 years old
% >100 years	% stands >100 years old
Mean stand age	Mean stand age
Mean cavity tree dbh	Mean dbh of all cavity trees
Cavity tree density	Cavity trees/km^2
Edge index	Length of edge between pole or older forest and non-forest/young forest in km/cumulative territory area in km^2
Access index	Length of linear corridors (roads, geophysical exploration lines, right of ways) in km/cumulative territory area in km^2
Fragmentation index	Edge + access length in km^2/cumulative territory area in km^2
Potential cavity tree density	Live trembling aspen/balsam poplar with decay + dead trees ≥30 cm dbh/km^2

Table 3.2. Annual and nesting season minimum convex polygon territory area (ha) for pileated woodpecker individuals and pair territories at Hinton Alberta, 1993–96.

			Annual MCP (June 1–May 31)								Nesting Season MCP (May 1–June 30)					
			1993–94		1994–95		1995–96		1993–96		1993		1994		1995	
Territory	Bird	Sex	*n*[a]	Area	*n*	Area	*n*	Area	*n*	Area	*n*	Area	*n*	Area	*n*	Area
Athabasca	9	F			321	1,116	167	2,129	488	2,288			8	58	74	299
	10[b]	M[c]			23	92			23	92			17	82		
	35	M			41	139	17	86	58	263					27	214
	Total				385	1,116	184	2,207	569	2,347			52	145	101	302
Black Cat	15	F			63	326			63	326			12	29		
	16	M			220	1,447	1		221	1,447			11	73	4	
	30	F			17	100	173	654	190	643					23	55
	Total				300	1,447	174	654	474	1,749			23	132	27	74
Bryan Creek	3	M			144	684	13	55	157	686			33	78	18	37
	4	F			72	1,177			72	1,177			20	61		
	25	F			33	143	110	649	143	686					40	202
	Total				249	1,667	123	663	372	1,929			53	145	52	202
Camp	18	M	244	782					244	782	47	289				
	11	M			142	733			142	733			17	60		
	12	F			232	915			232	915			14	155	4	9
	28	M					120	468	120	467					1	
	37	F							9	7						
	Total		244	782	374	1,124	120	468	747	1,348	47	289	31	176	6	18
Cold Creek	23	F					56	1,344	56	1,504					12	48
	24	M					130	1,564	143	686					22	244
	All						186	2,014	199	2,014					40	309
East Flats	13	M			72	756			72	756			21	62		
	14	F			80	576			80	576			32	231		
	Total				152	891			152	891			53	282		
Everest	31	F					169	1,803	169	1,803					46	172
	32	M					281	1,828	282	1,828					48	43
	Total						350	2,221	451	2,221					94	232
Fish Creek	10[a]	M			249	1,791	145	2,474	394	2,852					48	203
	27	F			26	189			26	189					14	53
	Total				519	1,791	145	2,474	410	2,852					62	204
Gaswell	7	M			143	1,731	106	1,816	249	2,294			37	457	4	2
	8	F			6	15			6	15			6	15		
	Total				149	1,731	106	1,991	255	2,336			43	676	4	142
Gregg Lake	21	M			109	806	132	1,929	241	2,127					65	596
	22	F			15	108			15	108					2	
	Total				124	806	132	1,929	256	2,127					67	596
Maxwell	1	F			239	1,580	188	2,646	427	3,117			44	132	56	108
	2	M			288	2,456	140	1,719	428	2,766			33	126	57	93
	Total				527	2,478	328	2,964	855	3,768			77	222	113	230
Pedley	17	M	54	59					54	59	59	11				
	33	F					230	316	281	316					60	83
	34	M					274	299	274	299					62	79
	Total		54	59			504	378	559	378	59	11			122	109
Prest Creek	5	F			191	1,978	138	3,185	329	3,807			26	123	7	22
	6	M			70	2,427			70	2,427			39	443		
	29	M					53	517	53	517					9	47
	Total						191	3,238	452	4,585			65	559	16	54
Solomon	36	F					150	1,649	150	1,649					24	131

[a] Number of radiotelemetry locations.

[b] Locations for bird 10 were divided between 2 territories because this bird left its original territory and mated with a different bird the next year.

[c] More than 1 bird of a given sex per territory indicates that the original bird died and was replaced by a new bird. Birds for each territory are listed in chronological order.

Table 3.3 Percent overlap of minimum convex polygon territories between mated birds and adjacent territories at Hinton, Alberta, 1993–96.

Category	Period	*n*	% Overlap range	$\bar{x}$	SE
Mated birds	Nesting period	6	62.5–92.3	81.0	13.3
	Annual 94–95	6	74.4–100.0	84.0	12.2
	Annual 95–96	5	78.9–93.7	87.1	6.0
	Total	10	66.4–100.0	85.7	11.2
Adjacent territories	Nesting period	13	0.0	0.0	0.0
	Annual 94–95	5	0–7.4	2.8	3.1
	Annual 95–96	8	0–13.2	1.7	4.7
	Total	11	0–12.8	4.2	4.9

Table 3.4. Alberta and northern British Columbia, pileated woodpecker nests, 1982–98.

	Year								
Location	1982 to 1991[a]	1992[a]	1993	1994	1995	1996	1997	1998	Total
Foothills Model Forest	5	11	12	18	21	28		9	113
Other Alberta areas	7	2	7	10	9	8			43
British Columbia					1	1			2
Total	12	13	19	28	31	37	9	9	158

[a] Nests reported by persons responding to requests for information about known pileated woodpecker nests prior to this study.

Table 3.5. Alberta pileated woodpecker clutch size and number of fledged young, 1990–98.

	Clutch size			Number of fledged young		
Year	3	4	5	0	2	3
1990		1			1	
1991		1				3
1992					3	1
1993		2			3	7
1994		13			6	15
1995	3	17		6	2	17
1996		19	1	1	10	15
1997		2	1		1	4
1998		5	4		3	6
Total	3	60	6	7	29	68

Table 3.6. Characteristics of radiotagged pileated woodpeckers at Hinton, Alberta, 1993–96.

Territory	Bird	Sex	Start Date	End Date	Days	End Status	Death Cause
Athabasca	9	F	29-May-94	18-Jun-96	751	alive	
Athabasca	38	F	24-Oct-95	30-Jan-96	98	dead	Northern goshawk
Black Cat	15	F	30-May-94	17-Nov-94	171	dead	Northern goshawk
Black Cat	16	M	02-Jun-94	17-Jun-95	380	dead	Northern goshawk
Black Cat	30	F	07-Jun-95	08-Jul-96	397	alive	
Bryan Creek	3	M	02-Jun-94	15-Feb-96	623	unknown	Unknown
Bryan Creek	4	F	30-May-94	26-Nov-94	180	dead	Northern goshawk
Bryan Creek	25	F	17-Apr-95	20-Jun-96	430	alive	
Camp	11	M	28-May-94	15-Feb-95	260	unknown	Unknown
Camp	12	F	31-May-94	14-Jun-95	379	dead	Northern goshawk
Camp	18	M	10-Jun-93	11-Nov-93	154	dead	Northern goshawk
Camp	28	M	30-May-95	18-Jun-96	385	alive	
Cold Creek	23	F	09-Apr-95	16-Nov-95	222	dead	Unknown mammal
Cold Creek	24	M	03-Jun-95	17-Jun-96	380	alive	
East Flats	13	M	31-May-94	04-Oct-94	126	dead	Unknown mammal
East Flats	14	F	03-Jun-94	15-Mar-95	285	unknown	Unknown
Everest	31	F	08-Jun-95	12-Jan-96	218	dead	Accident
Everest	32	M	01-Jun-95	23-Jun-96	388	alive	
Fish Creek	10	M	31-May-94	18-Jun-96	749	alive	
Fish Creek	27	F	07-Jun-95	12-Jun-95	5	dead	Northern goshawk
Gaswell	7	M	31-May-94	23-Jun-96	754	alive	
Gaswell	8	F	29-May-94	07-Jun-94	9	dead	Northern goshawk
Gaswell	26	F	02-Jun-95	23-Jun-96	387	alive	
Gregg Lake	21	M	29-Mar-95	22-Feb-96	330	dead	Northern goshawk
Maxwell Lake	1	F	31-May-94	30-Jun-96	761	alive	
Maxwell Lake	2	M	29-May-94	30-Jun-96	763	alive	
Pedley	17	M	11-Jun-93	26-Jun-93	14	dead	Northern goshawk
Pedley	33	F	03-Jun-95	06-Jul-96	399	alive	
Pedley	34	M	08-Jun-95	18-Jun-96	376	alive	
Prest Creek	5	F	30-May-94	20-Jun-96	751	alive	
Prest Creek	6	M	28-May-94	10-Oct-94	135	dead	Northern goshawk
Prest Creek	29	M	01-Jun-95	02-Jun-96	367	alive	
Solomon	36	F	22-Jun-95	19-Jul-96	393	alive	

Table 3.7. Habitat characteristics related to pileated woodpecker pair territory size (n = 14) with Pearson correlation and regression at Hinton, Alberta.

Habitat variable	Range	$\bar{x}$	SE	r	r^2
Mean tree dbh	13.4–19.4	16.1	1.9	-0.35	0.13
% deciduous + mixed	6.1–68.5	35.6	19.2	-0.21	0.04
% lowland spruce	1.3–34.4	10.2	9.2	0.32	0.13
% upland coniferous	15.6–87.3	45.5	19.4	0.06	0.00
% upland	42.5–94.8	73.0	13.8	-0.54[a]	0.25
% pole + mature + old	63.9–99.4	84.5	10.0	-0.43	0.19
% non-forest + young	0.6–36.1	15.5	10.0	0.43	0.19
Tree density	640.3–1,154.0	824.7	151.7	0.10	0.01
% forest cover	71.7–99.4	91.3	8.0	0.06	0.00
Large dead tree density	1.3–1.7	1.8	0.6	-0.21	0.04
Potential winter foraging substrate density	4.1–14.1	8.7	2.9	-0.75[a]	0.56[b]
Dead tree density	15.2–47.4	26.6	10.2	-0.12	0.01
Medium tree density	137.6–389.9	261.9	72.8	-0.24	0.06
Large tree density	55.9–161.7	111.8	32.9	-0.41	0.17
% trembling aspen	0.2–35.9	14.0	9.6	-0.03	0.00
% white spruce	2.2–46.2	26.0	14.7	-0.46	0.22
% trembling aspen + white spruce	7.2–62.5	40.0	19.3	-0.37	0.14
% tall stands	25.1–74.0	43.8	14.7	-0.25	0.06
% stands ≥7 m	74.2–99.4	92.9	6.8	-0.88[a]	0.78[b]
Mean stand height	10.3–20.6	14.1	3.0	-0.40	0.16
% closed stands	53.3–90.2	70.8	11.4	-0.37	0.14
Mean canopy closure	34.5–52.1	40.8	5.0	-0.26	0.07
% ≤50 years	0.0–49.5	18.9	17.1	0.16	0.05
% >75 years	30.7–93.1	59.1	19.4	-0.25	0.01
% >100 years	18.2 – 80.7	47.7	20.7	-0.12	0.02
Mean stand age	64.1–124.4	85.1	18.0	-0.28	0.07
Mean cavity tree dbh	40.9–52.1	45.6	3.5	-0.07	0.00
Cavity tree density	0.2–10.6	1.8	2.7	-0.56[a]	0.32
Edge index	0.2–1.7	0.8	0.6	0.08	0.01
Access index	1.3–5.5	3.5	1.4	0.25	0.06
Fragmentation index	1.4–6.7	4.4	1.6	0.24	0.24
Potential cavity tree density	5.5–55.1	23.1	13.1	-0.83[a]	0.69[b]

[a] significant correlation, $P \leq 0.05$.

[b] significant regression, $P \leq 0.05$.

Table 3.8. Pearson correlation values of relationships among habitat characteristics that were significantly correlated with pileated woodpecker pair territory size (n = 14) at Hinton, Alberta. P-values are listed below the correlation values.

Habitat characteristics	Habitat characteristics			
	UPFOR[a]	WFOR[b]	CAVD[c]	PCAVD[d]
WFOR	0.69			
	(0.003)			
CAVD	-0.01	0.48		
	(0.76)	(0.06)		
PCAVD	0.22	0.55	0.79	
	(0.32)	(0.03)	(<0.001)	
PCTGT7M[e]	0.74	0.71	0.29	0.68
	(0.009)	(0.004)	(0.311)	(0.011)

[a] % upland forest.
[b] Potential winter foraging substrate density.
[c] Potential cavity tree density.
[d] % stands ≥7 m tall.

Table 3.9. Pileated woodpecker productivity and mortality in the 7 smallest and 7 largest nesting season and cumulative pair territories at Hinton, Alberta, 1993–98.

Variable	7 smallest territories[a]			7 largest territories[a]			P value
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	
Clutch size (eggs/nest)							
Nesting season	21	4.10	0.00	21	4.10	0.30	0.500
Cumulative	24	4.17	0.38	18	4.0	0.00	0.036
Fledging success (young/nest)							
Nesting season	21	2.48	1.08	23	2.57	0.90	0.383
Cumulative	25	2.68	0.85	19	2.32	1.11	0.112
Nesting success (%)							
Nesting season	22	90.9	0.08	26	92.3	0.16	0.454
Cumulative	27	97.2	0.07	21	91.7	0.14	0.201
Mortality (deaths/week)							
Nesting season	170[b]	0.014	0.018	184	0.029	0.000	0.202
Cumulative	812	0.014	0.007	867	0.008	0.010	0.132

[a] Territories (n = 14) were divided into the 7 smallest and the 7 largest minimum convex polygon (MCP) areas for the nesting season and for cumulative (all points for all birds in the territory) radiotelemetry points.
[b] Number of weeks during the season that birds were exposed to mortality risk.

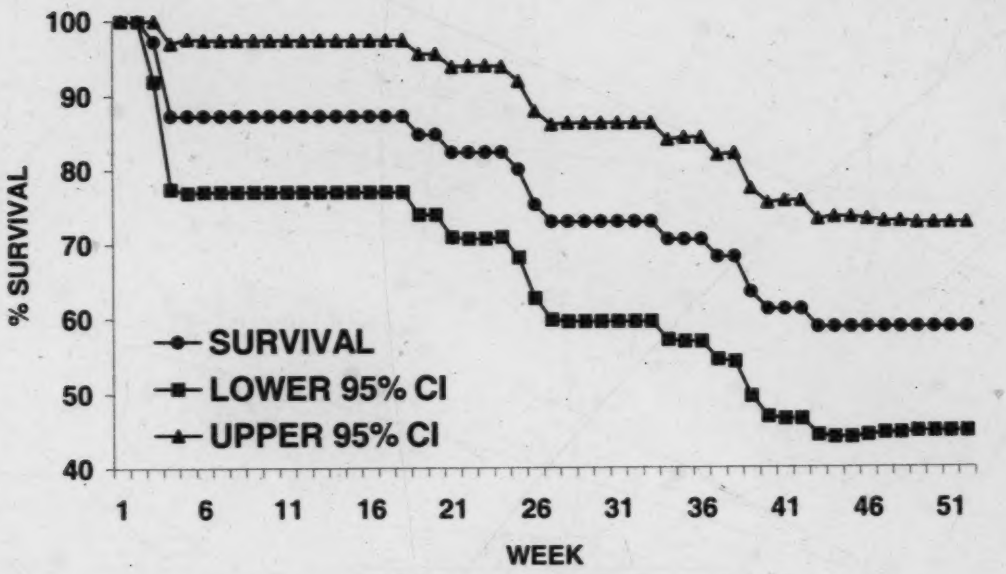

Fig. 3.1. Weekly survival of radiotagged adult pileated woodpeckers (n = 33) at Hinton, Alberta, Data are 3 years combined from June 1, 1993–June 1, 1996. June 1 was selected as week 1 because this was the approximate date that eggs hatched and adults were radiotagged.

4. AVAILABILITY OF PILEATED WOODPECKER CAVITIES AND USE BY OTHER SPECIES[1]

Cavity-nesting bird communities may be structured in webs, analogous to food webs, with cavities as the central resource around which interspecific and intraspecific interactions occur (Martin and Eadie 1999). If so, our understanding of wildlife communities can be increased by determining cavity use relationships among species. In a web structure, a species may have disproportionate importance if it supports a key structural component of the cavity resource. Cavity size (entrance dimensions and internal volume) may be a critical factor. McLaren (1963) divided the cavity-using wildlife community in the Cariboo Parkland region of British Columbia into 3 "cycles" (webs) according to cavity size associated with a primary cavity excavator species (PCE) and the secondary cavity user species (SCU) that used them: the small cavity web of the yellow-bellied sapsucker (*Sphyrapicus varius*), the midsize cavity web of the northern flicker (*Colaptes auratus*), and the large cavity web of the pileated woodpecker.

Pileated woodpeckers produce few cavities in comparison to other PCE (Harestad and Keisker 1989, Martin and Eadie 1999), but they may function as a keystone species (Power et al. 1996) by providing a critical source of large cavities for SCU that cannot enter smaller cavities excavated by other PCE. In boreal forests, volumes and entrance dimensions of pileated woodpecker cavities are more than twice as large as those of the northern flicker, the next largest PCE.

Each pair of pileated woodpeckers usually excavates a new nest cavity each year (Short 1982), and individuals may also excavate separate cavities or entrances into natural cavities for roosting (Hoyt 1957, Bull et al. 1992). Existing information about availability of pileated woodpecker cavities and use by other species is anecdotal (Hoyt 1948, 1957; McClelland 1977; Bull and Snider 1993; Hayward et al. 1993; Bull and Jackson 1995). I studied production, availability, and use of pileated woodpecker cavities to develop a better understanding of the ecological role of pileated woodpeckers in conserving cavity-using wildlife communities in western boreal forests.

STUDY AREA

The study area was the 26,000-km^2 Foothills Model Forest in the Rocky Mountain and Foothills Natural Regions of west-central Alberta, Canada (Beckingham et al. 1996). Information about cavity use was also obtained on an opportunistic basis from forested areas of central and northern Alberta and central British Columbia. Most information was obtained within 14 territories of radiotagged pairs of pileated woodpeckers within approximately 50 km of Hinton, Alberta (127°46'N, 117°39'W). Forests above 1,150 m were dominated by lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*). Below 1,150 m, mixed forests were codominated by lodgepole pine, trembling aspen (*Populus tremuloides*), white spruce (*P. glauca*), and balsam poplar (*Populus balsamifera*) (Beckingham et al. 1996). Other common tree species included black spruce (*Picea mariana*) and subalpine fir (*Abies lasiocarpa*). Forests contained 12% young (<30 years), 30% pole (31–100 years), 52% mature (101–160 years) and 6% old (>160 years old) trees.

METHODS

Cavity Production and Availability

I located cavity trees from 1993–1998 by following unmarked and radiotagged pileated woodpeckers, searching, and listening for adult and nestling calls. I attempted to locate all cavity trees within 14 territories by following 32 radiotagged pileated woodpeckers and searching, with

[1] A version of this chapter has been published: Bonar, R. L. 2000. Availability of pileated woodpecker cavities and use by other species. Journal of Wildlife Management 64:52–59.

total effort equivalent to 2,022 8-hour person-days. Radiotagged birds, followed every 2–10 days for approximately 0.5 day each over periods of 9–763 days, often visited cavity trees during the day and always roosted in cavity trees at night. Searches for cavity trees in 1993 were conducted by walking parallel transects in a grid pattern, with systematic coverage of all areas searched. This method was inefficient, so from 1994 to 1998 I used aerial photos and forest inventory information to identify stands in territories that were likely to contain large living or dead trembling aspen or balsam poplar trees and large conifer snags, which were identified as most likely to have pileated woodpecker cavities based on 1993 surveys. I was not able to search all likely stands, but I did search >75% of those identified in each territory; total effort ranged from 64–306 days/territory, and 11 of 14 territories received ≥115 days of effort. Mean density of cavity trees was estimated by dividing the total minimum convex polygon area of pair territories by the number of known cavity trees, and mean cavity density was estimated by multiplying mean cavity tree density times the average number of cavities/tree.

Cavity trees found using radiotelemetry were similar to trees found using other methods, so all cavity trees found within the study area were used in the analysis. I used a ladder or climbing spurs to inspect and measure 62% of cavity trees. A cavity was defined as any opening into a tree excavated by pileated woodpeckers with entrance dimensions similar to those of completed nest cavities. All other pileated woodpecker excavations started in suitable trees at positions similar to cavities were defined as cavity starts. Cavities were further classified by depth: shelf = entrance >12 cm into tree but no depth below entrance sill; shallow = depth 1–20 cm below entrance sill; deep = depth 21–55 cm; hollow = depth >55 cm. Hollow cavities were usually formed by a combination of pileated woodpecker excavation and fungal decay.

Cavity-tree locations were mapped and trees were revisited at irregular intervals to survey cavity availability and use. Most visits (n = 3,426) were during daylight, with approximately 20% at dusk or dawn. Changes since the last visit were recorded: number of cavities by depth class; tree standing or fallen; tree living or dead; complete or broken trunk. I determined the cause of changes where possible and the approximate date or season of major changes in condition. I estimated when changes had occurred by the position of excavated chips in relation to leaf fall. Production of new cavities was estimated by monitoring known cavity trees and activity of radiotagged pileated woodpeckers. I estimated annual production and loss of cavity trees and cavities using 1 June as a cutoff date; most new cavities in any given year had been completed by this date.

I estimated the availability of large natural cavities, those at least as large as cavities excavated by pileated woodpeckers, using 2 methods. First, I looked for large natural cavities in conjunction with other fieldwork, including following radiotagged pileated woodpeckers and cavity tree searching. Second, I looked for large natural cavities in all trees >25 cm dbh (n = 6,298) on 504 0.04-ha plots. Half of the plots were centered on arbitrarily selected cavity trees, and each of these was paired with a plot located using a random numbers table to select repeatedly a compass bearing and distance (measured by pacing) from the cavity tree until the plot location fell within the cavity-tree stand. Random plots were centred on the closest tree to the plot location.

Cavity Use

Pileated woodpecker and SCU use of cavities was determined by following radiotagged pileated woodpeckers to roosts, climbing trees to inspect cavities, watching cavities from the ground, scratching or knocking on cavity trees while watching the cavity entrance from the ground, and searching for evidence of cavity use (wood chips, feathers, droppings, nest materials) at the base of trees. I located radiotagged pileated woodpeckers at night at intervals of 1–15 days to identify their roost cavities. All direct or indirect observations of use were recorded each time a cavity was inspected. Direct observations included animals, eggs, and young. Indirect observations included droppings, castings, nest material, hair, and feathers.

To determine SCU occupancy (animal in cavity or observed leaving it at time of visit), I visually inspected 1,144 cavities and scratched or knocked on trees containing an additional

4,610 cavities (number corrected for multiple entrances) between 1 January 1993 and 30 June 1998. Trees were scratched before they were climbed for cavity inspection, and animals occupying cavities usually left the cavity or looked out, so I combined all data. I used a chi-square goodness-of-fit analysis coupled with Bonferroni confidence intervals (Neu et al. 1974) to test for seasonal differences in cavity occupancy rates. Cavities were not considered available for SCU when pileated woodpeckers were using them for nesting.

RESULTS

Cavity Availability

I found 611 trees containing 1,317 cavity entrances excavated by pileated woodpeckers (range 1–11 entrances/tree, (2.16 ± 1.63, $\bar{x} \pm$ SE). Of these, I climbed 379 trees and measured 686 separate cavities (shelf = 90; shallow = 76; deep = 445; hollow = 75) associated with 787 entrances. Because 11% ($n = 75$) of measured cavities had more than 1 entrance, I estimated that 1,172 separate cavities were available.

I found 339 cavity trees (range 4–48 trees/territory) in 14 territories delineated by following radiotagged pileated woodpeckers. Average cavity-tree density on territories was 1.28 trees/km^2 and average availability of cavities was 2.20 cavities/km^2. These are minimum estimates, because the number of cavity trees found in each territory continued to increase with the length of time radiotagged birds were monitored and was still increasing at the end of the study. Cavity trees tended to be clumped in distribution, with some stands containing many cavity trees while similar stands had none.

Pileated woodpeckers were responsible for almost all of the accessible large cavities available in the study area. Large natural cavities with entrances comparable in size to entrances made by pileated woodpeckers were rare. Only 15 large natural cavities were found in 2,022 person-days of fieldwork, and no large natural cavities were found in large trees within sample plots.

Cavity Recruitment and Loss

Radiotagged pileated woodpecker pairs initiated as many as 22 new cavity starts/pair/year in the February–May nesting season, but most cavity starts were abandoned within a few minutes after just a shallow excavation had been completed. An average of 0.2 starts/pair/year were continued to the shelf or shallow cavity stage and then abandoned. Renewed excavation at cavity starts or shelf–shallow cavities started in previous years was common, and these were sometimes completed and used for nesting (22% of 158 nest cavities). However, each pair normally excavated only 1 complete nest cavity/year. On 3 occasions, an existing cavity was used for nesting without further excavation. Cavity excavation outside of the nesting season was rare. I found 5 cavity entrances excavated between November and March that either extended existing cavities or created a new entrance into an internal roosting hollow. In total, each pair produced an average of 1.2 cavities/year.

The primary cause of cavity loss was wind events that caused tree fall or trunk breakage at or below a cavity. Natural cavity deterioration was rare because most cavities were excavated into living trees with healthy sapwood. Compartmentalization of injury by living trees (Sedgwick and Knopf 1991) was rare because pileated woodpeckers regularly removed grown-in edges of cavity entrances in living trees. They also maintained roost cavities by removing wood chips and material deposited by other species.

New cavities of pileated woodpeckers were produced at an annual rate of 0.06 cavities/km^2, estimated by dividing the observed cavity production rate of 1.2 cavities/pair/year by the observed average of 18.9 km^2/pair territory. Cavity recruitment in the 14 territories exceeded cavity loss during the study: 17 new shelf–shallow cavities and 84 new deep cavities were excavated, and 4 shelf–shallow, 36 deep, and 2 hollow cavities were lost.

Cavity Use

I obtained 762 roosting locations for 32 radiotagged pileated woodpeckers in 14 territories from June 1993 to June 1996. Radiotagged birds roosted in 240 separate cavities in 185 cavity trees. Based on evidence (droppings, feathers) found within cavities or at the base of trees, pileated woodpeckers also roosted in an additional 32 cavities in 28 trees within the 14 territories. These roosts may have been used by the radiotagged territorial pair, their offspring, or nonbreeding floater birds, which were detected in several territories. In total, at least 62.8% of cavity trees within pair territories (n = 339) were used as roosts. Overall, evidence of pileated woodpecker roosting was found inside 44.6% of visually inspected cavities (Table 4.1). However, 43 roost cavities used by radiotagged birds were empty when visually inspected, so roosting evidence within cavities underestimated the actual proportion of cavity trees used for roosting. Considering all available evidence (radiotelemetry, evidence within cavities and at base of tree, direct observation), at least 61.7% of all cavity trees (n = 611) were confirmed as pileated woodpecker roost trees. Pileated woodpeckers did not use shelf cavities for roosting and rarely roosted in shallow cavities. At least 50.9% of deep cavities and 95.8% of hollow cavities were used for roosting (Table 4.1).

Cavity occupancy by other species was significantly higher than expected in May and significantly lower than expected in January, February, July, August, and November (Fig. 4.1). The May peak corresponded to the period of reproduction, which was the only time some other species used pileated woodpecker cavities. Although cavity occupancy was low, 53.5% of inspected cavities contained evidence of use by at least 1 SCU. Bats, owls, and squirrels used 41.7% of shelf and shallow cavities (Table 4.1). These usually contained fecal material, indicating they were probably used primarily for shelter and roosting. Wasps built nests mainly in shelf cavities. Owls, squirrels, ducks, and northern flickers nested in 42.8% of deep cavities, and owls and squirrels nested in 14.1% of shallow cavities. The SCU sometimes used pileated woodpecker cavities for food storage; 8 cavities contained recently killed small mammals, which were probably deposited by owls. Red squirrels (*Tamiasciurus hudsonicus*) filled 1 deep cavity with dried mushrooms and 2 hollow cavities with conifer cones.

Most SCU leave evidence of their use in cavities (Peterson and Gauthier 1985). It was sometimes difficult to estimate age of material inside cavities, so I used occupancy combined with fresh material to estimate temporal demand for pileated woodpecker cavities (Fig. 4.2). Five SCU used pileated woodpecker cavities year-around and 10 SCU used them only during the summer (Fig. 4.2). The number of SCU using pileated woodpecker cavities peaked in May–June and was lowest in November–February.

Pileated woodpecker cavities were used by at least 18 SCU (Fig. 4.2). Based on binocular observation, bat species that used pileated woodpecker cavities were the little brown bat (*Myotis lucifugus*), silver-haired bat (*Lasionycteris noctivagans*), and big brown bat (*Eptesicus fuscus*). Six other species were observed using cavities excavated by other PCE in trees containing pileated woodpecker cavities: yellow-bellied sapsucker, red-breasted nuthatch (*Sitta canadensis*), black-capped chickadee (*Poecile atricapillus*), mountain bluebird (*Sialia currucoides*), least chipmunk (*Tamias minimus*), and ermine (*Mustela erminea*). These species may also have used the pileated woodpecker cavities.

Interspecific Interactions

I did not observe direct competition between species for pileated woodpecker cavities. Pileated woodpeckers aggressively harassed red squirrels, northern saw-whet owls (*Aegolius acadicus*), and boreal owls (*A. funereus*) if these species closely approached their nest, but they also tolerated other species using cavities in or near the nest tree if they were not close to the nest cavity. I did not observe concurrent nesting use of cavity trees by pileated woodpeckers and other PCE, but 12 pileated woodpecker cavities and 4 other PCE cavities in trees containing active pileated woodpecker nests were used by 5 SCU: Barrow's goldeneye (*Bucephala*

islandica), northern saw-whet owl, northern flying squirrel (*Glaucomys sabrinus*), red-breasted nuthatch, and black-capped chickadee. Cavities or cavity entrances excavated by northern flickers ($n = 38$), hairy woodpeckers *(Picoides villosus*) or three-toed woodpeckers (*P. tridactylus*, $n = 29$), and yellow-bellied sapsuckers ($n = 18$) were present in 13.9% of pileated woodpecker cavity trees.

Pileated woodpeckers sometimes roosted in an empty cavity in multiple-cavity trees when another cavity was being used by a SCU ($n = 15$, 2.4% of visual roosting locations), but they usually roosted in trees with unoccupied cavities. I saw pileated woodpeckers attempting to roost in cavities occupied by northern saw-whet owl ($n = 2$), northern flicker ($n = 2$), northern flying squirrel ($n = 3$), and hairy woodpecker ($n = 1$), but in each instance the pileated woodpecker immediately flew to another roost after it looked into the cavity and discovered the occupant. Two instances of roost cavity sharing were observed. A female pileated woodpecker entered and roosted in a hollow that was already occupied by a roosting male hairy woodpecker, and a female northern flicker entered and roosted in a hollow that was already occupied by a roosting female pileated woodpecker.

Alternating use of pileated woodpecker cavities by pileated woodpeckers and SCU was common. Almost half (49.3%) of inspected cavities contained evidence of use by more than 1 species. Pileated woodpeckers ($n = 9$), red squirrels ($n = 2$), and northern flying squirrels ($n = 2$) were observed removing material deposited by other species from cavities, and removed material was commonly found at the base of cavity trees.

DISCUSSION

Cavity Availability

Annual cavity production by each pair of pileated woodpeckers was similar to rates for other woodpecker species (Short 1982). However, pileated woodpeckers produce fewer cavities per unit area than the combined production of other PCE. In 2 British Columbia studies, pileated woodpeckers were responsible for only 2.0% (Martin and Eadie 1999) and 3.2% (Harestad and Keisker 1989) of PCE nests.

Low production rates of cavities by pileated woodpeckers were partially offset by low rates of cavity tree loss, which averaged 1.1% annually in this study and 1.7% in Oregon (Bull 1987). McClelland (1977) reported 5.4% annual loss of cavity trees produced by 7 other PCE, and Sedgwick and Knopf (1992) reported annual cavity tree loss of 23.0% in cottonwood bottomlands. Pileated woodpeckers excavate cavities in large trees (McClelland 1979, Bull 1987), which remain standing longer than smaller trees (Bull 1983) used by other PCE (Bull et al. 1986, Harestad and Keisker 1989). Like other woodpeckers, pileated woodpeckers prefer to excavate cavities in trees softened by fungal decay (Conner et al. 1975, 1976; Bull et al. 1992). I believe the main reason for low pileated woodpecker cavity tree loss rates in this study was because 77.1% of cavity trees were living. Heart rot fungi infected all cavity trees, but living sapwood probably served to delay trunk breakage. I found up to 90 pileated woodpecker cavities in a single pair's territory, indicating that cavities in living trees may persist for many decades.

Despite low rates of loss, pileated woodpecker cavities were an uncommon resource when compared to availability of cavities excavated by other PCE. Average density of pileated woodpecker cavity trees was 1.28 trees/km^2 in the study area. By comparison, Dobkin et al. (1995) reported 453 PCE cavity trees/km^2 in Oregon riparian and snowpocket aspen forests, and Harestad and Keisker (1989) found 233 PCE nests/km^2 in interior British Columbia.

Cavity Use

Cavity availability and interspecific competition may limit the abundance of the SCU community (von Haartman 1957, Brush 1983, Brawn and Balda 1988, Bock et al. 1992, but see Waters et al. 1990). Pileated woodpeckers roosted in >60% of their own cavities over a 5-year period, but used only a small fraction of available cavities for roosting on any given night or during

any season. Each pileated woodpecker had several roost trees and usually flew directly to another roost if disturbed or if a roost was occupied. Cavity use was high as determined by observed evidence, particularly for deep and hollow cavities, but 22.3% of cavities were empty when inspected, and empty cavities were present throughout the year. However, empty cavities did not necessarily imply nonuse, because pileated woodpeckers and SCU used empty cavities without leaving evidence, and they also removed evidence of use from cavities. Cavity occupancy was low, and I did not observe any direct competition between species for cavities. Considering all evidence, I believe that there was a surplus of pileated woodpecker cavities available for SCU use in the study area during all seasons.

Cavities excavated by pileated woodpeckers were associated with a high diversity of cavity-using species. Pileated woodpecker cavities were used or probably used by 61% of 38 cavity-using vertebrate species in the study area. Three of 16 cavity-using vertebrate species that did not use pileated woodpecker cavities were too large to enter them and 10 other species were uncommon in the study area. At least 38 species of vertebrates are known to use pileated woodpecker cavities (Hoyt 1957, Ehrlich et al. 1988, Bull and Snider 1993, McClelland 1977, Bull and Jackson 1995, this study). The next largest reported SCU community for a North American PCE was 24 species associated with red-cockaded woodpecker (*Picoides borealis*) cavities (Conner et al. 1997). Many species that used red-cockaded woodpecker cavities did so only after they had been enlarged by pileated woodpeckers (Conner et al. 1997). Collectively, cavities of other PCE occurring in my study area were used by at least 13 SCU (R. L. Bonar, unpublished data).

Many SCU that can enter smaller cavities also used pileated woodpecker cavities, which are larger, deeper, and often higher above ground than other PCE cavities in the study area. Large entrances and cavity volume make pileated woodpecker cavities accessible to more species than smaller cavities excavated by other PCE. Large cavities can increase reproductive success and reduce predation risk (Moed and Dawson 1979, Rendell and Robertson 1989, Li and Martin 1991), and may provide thermoregulatory advantages for some species, including northern flying squirrels (Carey et al. 1997). Conversely, large entrances may actually increase predation risk and competition for cavities (Moed and Dawson 1979). Use of pileated woodpecker cavities by SCU may also have been influenced by the availability of other cavities and by selection criteria and other habitat characteristics of SCU.

I found evidence to support McLaren's (1963) concept of a large cavity web based on pileated woodpecker cavities. Pileated woodpeckers produce large cavities, which were used by 4 large SCU: Barrow's goldeneye, common goldeneye *(B. clangula)*, boreal owl, and American marten *(Martes americana)*. As these species are too large to enter most other PCE cavities, they depend on either pileated woodpecker cavities or large natural cavities. My results also support the concept of a cavity web structured around cavities as a central resource (Martin and Eadie 1999). Based on cavity size, the pileated woodpecker cavity web provides a critical resource for large SCU when natural cavities are rare, as they were in the study area. Smaller species also used pileated woodpecker cavities, indicating probable linkages between the pileated woodpecker cavity web and webs based on smaller PCE cavities.

MANAGEMENT IMPLICATIONS

Pileated woodpecker cavities are an important resource for the cavity-using wildlife community and may be a critical resource for some large SCU in boreal forests. On that basis, pileated woodpeckers are a keystone species, with an essential functional role in maintaining the cavity-using wildlife community in boreal forests. Further research on species-specific cavity selection and use would help to determine functional relationships between PCE and SCU.

While there may have been a surplus of pileated woodpecker cavities in this study, potential increases in losses from fires, logging, and other disturbances could interact to reverse the current situation. It could take many years to replace lost cavities because of low rates of cavity production. As pileated woodpecker cavity trees can persist as a cavity user resource for many years, perhaps several decades, forest managers should attempt to identify and protect existing

pileated woodpecker cavity trees. Habitat conservation strategies that include a continuing supply of trees suitable for future cavity production should be developed to ensure continued production of new pileated woodpecker cavities.

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Table 4.1. Species, use category, and % use, determined by cavity inspection, of pileated woodpecker cavities in forests near Hinton, Alberta, 1993–98.

		Cavity type (% use)				
Species	Use category[a]	Shelf (n = 115)	Shallow (n = 97)	Deep (n = 570)	Hollow (n = 96)	Total[b] (n = 878)
Pileated woodpecker[c]	Ro	0.0	10.3	50.9	95.8	44.6
Secondary cavity users						
Duck	Re	0.0	0.0	12.1	3.1	8.2
Squirrel	Re, Sh, Fs,	13.0	10.3	14.7	2.1	12.3
Owl	Re, Sh, Fs, Ro	15.7	26.8	18.1	0.0	16.6
Bat	Ro	13.0	3.1	2.5	5.2	5.4
Woodpecker	Re, Ro, Sh	0.9	2.1	1.8	13.5	2.8
Unknown mammal	Un	8.7	11.3	8.4	10.4	8.3
Unknown bird	Un	4.3	8.2	9.8	17.7	9.8
Unknown species	Un	3.5	0.0	1.8	7.3	1.9
Wasps	Re	6.1	2.1	0.4	0.0	1.3
Total SCU species		65.2	63.9	69.5	59.4	67.2
Empty		34.8	33.0	21.1	4.2	22.3

[a] Use category: Ro = roosting, Re = reproduction, Sh = shelter, Fs = food storage, Un = unknown.

[b] Total use exceeds 100% because of cavities that contained evidence of multiple species use

[c] Excludes pileated woodpecker nesting activity.

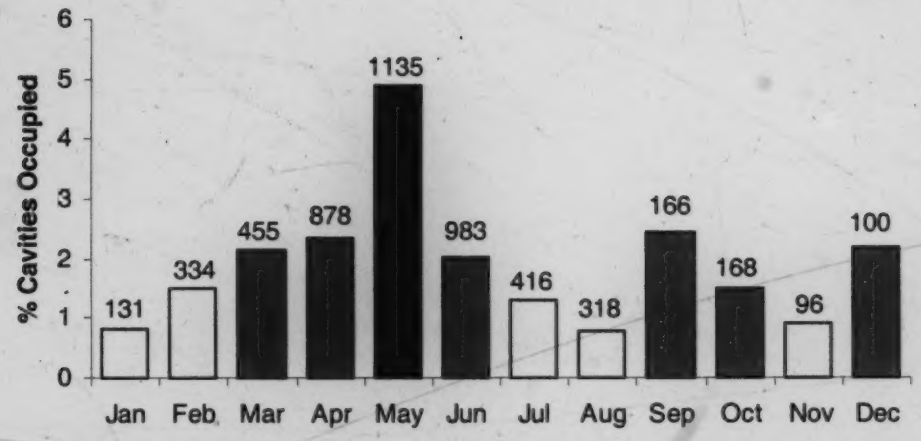

Fig. 4.1. Monthly % occupancy of pileated woodpecker cavities in forests near Hinton, Alberta, 1993–98. Darkest bar indicates significantly ($P < 0.05$) higher than expected occupancy, grey bars indicate use not significantly different than expected, white bars indicate significantly lower than expected occupancy, assuming uniform yearly occupancy. Sample size is shown above each bar.

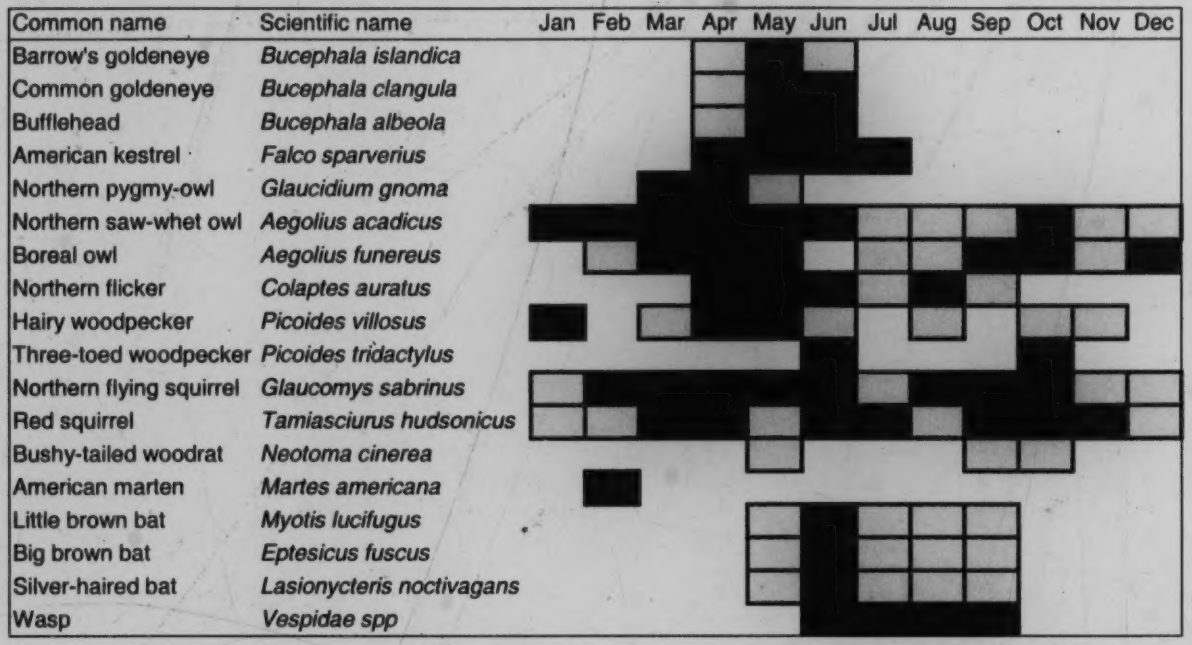

Fig. 4.2. Monthly occurrence of species (dark boxes) and fresh evidence of species (light boxes) found inside pileated woodpecker cavities in forests near Hinton, Alberta, 1993–98. Occurrence was defined as an animal observed inside, entering, or leaving a cavity, and fresh evidence was defined as droppings, hair, feathers, fecal material, nest material, eggs, or other indirect evidence of use.

5. GENERAL DISCUSSION AND CONCLUSIONS

PILEATED WOODPECKER HABITAT ECOLOGY IN THE ALBERTA FOOTHILLS

Pileated woodpeckers (*Dryocopus pileateus*) are specialist predators of wood-dwelling ants, especially carpenter ants (*Camponotus spp*). In Alberta, as in other areas, they preferred to forage on large (≥25 cm dbh) wood substrates containing carpenter ants. Forest characteristics vary considerably across the range of pileated woodpeckers (Bull and Jackson 1995, Kirk and Naylor 1996) but preference for carpenter ants found in large substrates that are either dead or damaged is a constant. Healthy trees were rarely used. In contrast, I found that habitat selection was very flexible at the territory and stand scales. Most available habitats were used and mature and old forests were not strongly preferred. This suggests that pileated woodpeckers select foraging habitat primarily because it contains food-bearing foraging substrates (Renken and Wiggers 1989, Rolstad et al. 1998), and that most other habitat characteristics are important only insofar as they correlate with foraging substrate (food) density. This conclusion explains why selection at the foraging substrate scale (Conner 1980, Bull et al. 1986, Bull and Holthausen 1993, Flemming et al. 1999) is stronger and more consistent between studies than selection at the forest characteristics scale (Renken and Wiggers 1989, Bull 1987, Mellen et al. 1992, Bull and Holthausen 1993). Pileated woodpeckers specialize on large dead or damaged trees, snags, stubs, logs, and stubs associated with the processes of tree death and decomposition in forests.

Predator avoidance behaviour may significantly modify foraging habitat use. Open, young forests regenerated after logging were avoided, probably because of a lack of escape cover (standing trees) in recent cutblocks. Cutblocks with residual trees and regenerated forests >7 m tall were used extensively. The probable importance of trees to facilitate predator avoidance has received little research attention but could be an important issue for forest managers interested in conserving pileated woodpeckers.

Patterns for nest and roost tree selection were similar to those described for foraging. The strongest selection was at the cavity tree and position on the cavity tree scales. Pileated woodpeckers preferred large (>35 cm dbh) trees with stem decay, especially living trembling aspen (*Populus tremuloides*) infected with the *Phellinus tremulae* fungus. All other forest characteristics associated with cavity trees were less strongly selected. This suggests that pileated woodpeckers select cavity trees primarily because of tree characteristics and that selection at other scales relates to the availability of potential cavity trees. Although there is considerable regional variation in cavity tree characteristics (Conner et al 1975, Bull 1987, McClelland 1979, Peck and James 1983, Mellen 1987, McClelland and McClelland 1999), common features of cavity trees in all regions are that they are large trees with stem decay. Variation in reported tree species, size, and decay characteristics probably reflects relative availability of potential cavity trees between forests more than a difference in preference.

Although pileated woodpeckers show regional flexibility in cavity tree selection, they show local preference for cavity tree characteristics when given a choice. In central Alberta and British Columbia boreal and cordilleran forests, living trembling aspens with stem decay were clearly preferred, although balsam poplar (*P. balsamifera*) and dead conifers were also used. The inter-relationships between aspen, *P. tremulae*, and pileated woodpeckers are significant because aspen is abundant in boreal forests. It grows rapidly, is relatively short-lived, and is prone to infection by *P. tremulae*, which is endemic throughout the range of aspen. In the absence of other disturbances, stem decay may be the proximate cause of aspen mortality (Hiratsuka et al. 1990). This process acts to benefit pileated woodpeckers in 2 ways: (1) it provides many trees that have suitable characteristics for cavities; and (2) it causes damage and leads to tree mortality, which in turn provides suitable colony-site characteristics for carpenter ants.

Similar to foraging habitat selection, predator avoidance was the only habitat factor that may significantly modify cavity tree selection. I believe that the small open area I observed around all cavity trees and the tendency for cavity trees to be located on stand edges probably served to minimize predation risk. The cavity tree provided opportunities for adults to escape avian predators while the open space surrounding it reduced opportunities for predators to exploit the nest. Although the "open space" hypothesis has not been previously reported for pileated woodpeckers, it has been noted for the congeneric black woodpecker (*Dryocopus martius*;

Rolstad et al. in review). Preference for relatively sound sapwood, smooth bark, and no branches near the cavity site may also be related to predator avoidance. Open areas would make it easier to see avian predators, especially the northern goshawk (*Accipiter gentilis*), which may take young at nest entrances (Bull and Holthausen 1993). Sound sapwood would help to prevent nest destruction by larger mammals such as bears. It has been suggested that pileated woodpeckers sometimes use utility poles as nest trees (Dennis 1964, Millar 1992) because they have few opportunities remaining in forests that have been impacted by human activities (Millar 1992, P. Ohanjanian, personal communication). I propose that a more likely alternative explanation is that pileated woodpeckers prefer openings around their nest trees to reduce predation risk, and that they are simply exploiting an opportunity when they nest in utility poles. Short (1979) agreed with this hypothesis and also thought that openings could serve to reduce competition from other species for cavities.

I found strong relationships between habitat quality variables and pair territory size. Smaller territories had higher densities of potential foraging substrates and cavity trees, and lower proportions of short (≤7 m) forest cover. Pileated woodpeckers in my study area had much larger territories than previously reported. Possible explanations for this in comparison to other regions include differences in winter severity and density of foraging substrates, which are probably directly related to food density. However, large territory size did not result in a reduction of fitness. Productivity and survival in my study area were higher than previously reported for pileated woodpeckers, and territory size and other habitat characteristics were independent of productivity and survival. This suggests that pileated woodpeckers are able to maintain fitness across a habitat quality gradient by increasing territory size. As the radiotelemetry portion of my study investigated habitat relationships with fitness across a relatively narrow gradient of forest area and forest age, further work is needed to determine habitat quality thresholds that would affect fitness. However, my cavity tree and productivity results, which were collected over a larger area, suggest that pileated woodpeckers can successfully reproduce and occupy landscapes with low (<10 %) amounts of forest cover. Another observation that may be important to this issue is the co-occurrence of pileated woodpeckers and their main predator, the northern goshawk. Goshawks do not prosper in landscapes with large amounts of young forest or non-forest (Reynolds et al. 1992, Squires and Reynolds 1997). Pileated woodpeckers that exploit such landscapes may be able to do so in the absence of their main predator and adult survival may actually increase when compared to birds living in forested landscapes that are exposed to goshawk predation.

Territory size, productivity, and adult survival were quite stable over the study period. Factors that could influence this apparent balance include climatic factors, changes in prey populations (especially carpenter ants), and changes in the abundance of foraging substrates. Inclement spring weather may influence nesting onset (K. Aubry and C. Raley, personal communication) and clutch size (Chapter 3), and winter severity could affect adult survival. Pileated woodpeckers take advantage of temporary food resources such as bark beetle outbreaks (Bull et al. 1986) but little is known about relative population stability of carpenter ants, which are their main prey. Carpenter ant populations may increase if suitable wood substrates are abundant, but other factors may also influence populations (Sanders 1964, 1970). Under natural disturbance regimes, substrates suitable for carpenter ants (and pileated woodpecker foraging) are most abundant for a few decades following major fire disturbance and in mature/old forests that have started to accumulate dead wood through endemic mortality (Lee et al. 1995).

If pileated woodpeckers are able to maintain fitness across a habitat gradient, the main effect of reductions in habitat quantity and quality appears to be a direct effect on population density, since territories are vigorously defended against other pileated woodpecker pairs. Declining habitat quality leads to larger territories, which in turn reduces the overall population density. In Alberta foothills forests pileated woodpecker populations appear to be structured in adjacent non-overlapping territories defended by mated pairs, with non-territorial birds existing as floaters within and between territories.

Annual territories, defended all year, were much larger than the area used during the nesting season. I believe that large annual territories were needed to support winter habitat requirements (Chapter 2). Pileated woodpeckers have generally been considered limited by nesting season requirements (Bull and Jackson 1995). I agree with McClelland (1979), who thought that reduced

food availability meant that winter was the limiting season for pileated woodpeckers. Further work to investigate population structure would provide additional insight into the reasons for seasonal territory size differences and limiting factors.

I provide the first quantitative evidence that pileated woodpecker cavities are an important resource for the cavity-using wildlife community and may be a critical resource for some large secondary cavity users in Alberta foothills forests. On that basis, pileated woodpeckers are a keystone species, with an essential functional role in maintaining the cavity-using wildlife community in forests. This confirms the findings of other researchers, who felt that pileated woodpecker cavities were important for secondary cavity users (McClelland 1979, Bull and Snider 1993). Further research on species-specific cavity selection and use would help to determine functional relationships between primary cavity excavators and secondary cavity users. Another area requiring more investigation is the long-term dynamics of pileated woodpecker cavity trees.

PILEATED WOODPECKERS AND FOREST BIODIVERSITY CONSERVATION

The role of research focused on individual forest species has changed considerably since the concept of biodiversity conservation rose in importance following the 1992 Convention on Biological Diversity[1]. Focus has shifted from game species, which traditionally drew attention because of their economic and social importance, to species at risk and species selected because people believed their prosperity would help to ensure the prosperity of other species. Much research has been oriented to this last group, which has variously been named indicator, keystone, flagship, and umbrella species. Although the scientific rationale for selecting individual species as representatives for others is equivocal (Landres et al. 1988), the concept remains popular with scientists and managers, who need practical tools to manage forests that support thousands of species (Simberloff 1998, Lindenmayer 1999). Interest in pileated woodpeckers has generally centered around 3 issues: (1) their potential role as indicators of mature/old forests; (2) their role in conserving cavity-using wildlife communities; and (3) concerns about negative effects of forest management, which could lead to the pileated woodpecker becoming a species at risk in the future. I discuss each of these issues below.

Pileated woodpeckers habitat selection is strongest for specific characteristics at the foraging substrate and cavity tree scales. This conclusion provides insight into the question of whether or not pileated woodpeckers are mature forest obligates (Robbins et al. 1989, Bull 1987, Mellen et al. 1992, Rolstad et al. 1998). I conclude that pileated woodpeckers are not mature forest obligates and they are not suitable indicators for mature/old forests because they use all forest ages. I suggest instead that they are obligates for large damaged or decayed wood substrates, which support reproduction, shelter, and food requirements. In that regard, pileated woodpeckers may be excellent indicators for forest function. Their presence and prosperity is an indicator that the structure, composition, and functions of tree death and decay are being maintained. Because pileated woodpeckers are associated with the largest wood substrates, it is likely that forests that support pileated woodpeckers will also support other species that depend on the processes of tree growth, death, and decay to meet their needs.

Pileated woodpecker cavities were used by most of the cavity-using wildlife community in the study area, and they may provide the primary source of large cavities in Alberta foothills forests because large natural cavities are generally rare. If trees suitable for pileated woodpecker cavities are conserved and pileated woodpeckers continue to excavate and maintain cavities, the cavity needs of most other primary cavity excavator species and many secondary cavity user species are likely to also be conserved. I suggest that prosperity of pileated woodpeckers would be a good indicator for the health of cavity-using wildlife communities. Addition of other primary cavity excavator species with pileated woodpeckers would probably improve the indicator. The importance of primary cavity excavators has been widely recognized (eg McClelland et al. 1979, Thomas et al. 1979, Raphael and White 1984, Carlson and Aulen 1990).

My results support the concept that pileated woodpeckers could be negatively impacted by certain forest management regimes. Specifically, management regimes that reduce the agents that cause tree mortality and the availability of dead wood could be detrimental over long periods.

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[1] United Nations Conference on Environment and Development (UNCED), June 1992.

Long-term prosperity of pileated woodpeckers depends on a continuing supply of large trees that can become foraging substrates and cavity trees.

Forest management regimes occur across a gradient from intensive, short-rotation plantations of fast-growing exotics such as *Eucalyptus* and *Acacia* species to extensive, variable aged regimes based on natural disturbance regimes. Management regimes within the range of the pileated woodpecker span a gradient from intensive short rotations of southern pine species in the southeastern United States to low-intensity variable management of native species in most Canadian boreal forests. However, there are few areas in North America within the range of the pileated woodpecker where extensive forest landscapes have had significant long-term reductions in damaged and dead large trees, and pileated woodpecker populations are generally healthy (Bull and Jackson 1995).

In Scandinavia the black woodpecker, which is similar to the pileated woodpecker in most ecological aspects, lives in forests that have been intensively managed for many decades (Gamlin 1988). Black woodpeckers successfully exploit these landscapes (Johnsson 1993, Tjernberg et al. 1993, Rolstad et al. 1998, Rolstad et al. in review), but other woodpecker species have declined, probably as a direct result of reduced amounts of dead wood and old deciduous forest (Angelstam 1990). Black woodpeckers have adjusted to reduced dead wood in managed Scandinavian forests by foraging on carpenter ants inhabiting stumps in logged areas (Rolstad et al. in review) and nesting in large residual trees retained in forest landscapes (Johnsson 1993, Rolstad et al. in review).

Although it is not currently possible to examine the effects of reduction in damaged and dead trees over large intensively managed forest areas in North America, a case can be made that pileated woodpeckers would adapt as black woodpeckers did in Scandinavia. Both species specialize on carpenter ants and show flexibility in cavity tree selection. However, it would not be prudent to assume that pileated woodpeckers or any other woodpecker species would adjust to severely altered forest composition and structure.

Managers interested in conserving pileated woodpeckers and other species that depend on tree cavities and dead wood must ensure that forests are managed to maintain these elements at some level. Unfortunately, the "how much is enough" question has not yet been answered – managers know that some amount of large dead wood must be maintained in forests to ensure ecological function, but they do not know how much is required. As every tree removed from natural forests for human use is a dead tree removed from the system, answers to this question have great economic and social importance. Managers must balance easily quantified benefits to people with difficult-to-quantify ecological benefits for species such as pileated woodpeckers. Additional observational research in lower-quality habitat or experiments to assess pileated woodpecker response to reductions in trees suitable for foraging substrates or cavity trees is warranted to investigate these questions.

Conservation of the dead wood resource in managed forests has usually been approached from two main directions. The traditional approach is to protect some areas and develop rules for retaining additional wood in managed areas. This approach may be effective, but it tends to reduce natural heterogeneity in forests. The second approach is to describe natural patterns of heterogeneity and the processes that create them, and then to manage to maintain the patterns through time (Bunnell and Huggard 1999). A major assumption to this approach is that human activities such as logging can be substituted at least in part for natural disturbances such as forest fire. Two supporting assumptions are: (1) that ecological response to a mechanical process such as logging will be similar to that of a chemical process such as fire; and (2) there is redundancy in forest ecosystems – some wood can be removed from the natural system without impairing function. The concept of adaptive management is touted as a way to correct management if desired outcomes do not occur.

Conservation of pileated woodpeckers in managed forests appears to be dependent on successful application of efforts to conserve large dead wood. Current trends, whether derived from rule-based or heterogeneity-based approaches, are to increase the quantity of living and dead structure in protected and managed areas. In particular, retention of trees, snags, and logs in harvest areas, and especially living trembling aspen infected with *P. tremulae*, will benefit pileated woodpeckers. These trends offer promise that pileated woodpeckers will be successfully

conserved in managed forests, without the need to see if their habitat flexibility is as strong as that of the black woodpecker in Scandinavia.

MANAGEMENT RECOMMENDATIONS FOR PILEATED WOODPECKER CONSERVATION IN MANAGED FORESTS

My research is applicable to Alberta foothills forests for general habitat ecology, and to central Alberta and British Columbia forests for cavity tree ecology. However, I believe that pileated woodpecker habitat ecology should be similar in forests with similar tree species composition, disturbance regimes, and climate. In particular, I expect that pileated woodpecker habitat ecology would be consistent with my results in western Canadian cordilleran, boreal, and sub-boreal forest regions. The following recommendations include a combination of my results and my own thoughts on what would be appropriate ranges. Forest managers should not interpret these recommendations as absolute numbers that must be achieved. They are more appropriately applied as general guidelines.

Conservation of pileated woodpeckers in managed forests should focus on long-term maintenance of large damaged and dead wood structure at both landscape and stand scales. I recommend using definitions of potential cavity trees as living or dead deciduous species and dead coniferous species ≥30 cm dbh and potential foraging substrates as snags, stubs, and defective/decayed living trees ≥20 cm dbh. These include 98% and 82% of used cavity trees and foraging substrates, respectively. I believe it is more important to manage for a larger proportion of used habitat structure than to manage only for habitat structures that are statistically selected. Although pileated woodpeckers used smaller trees as cavity trees, they clearly preferred larger trees, and large deciduous trees have higher levels of stem decay than smaller trees. Living deciduous trees with external decay indicators, especially fungal conks, have the highest potential value. Logs and stumps are also important as foraging substrates in summer, but the focus should be on standing substrates, which are a critical resource in winter. Because pileated woodpecker pairs defend exclusive territories, an appropriate management scale for provision of habitat should approximate the average size of pileated woodpecker territories, about 2,000 ha. Management of numerous 2,000 ha units across forest landscapes is needed to sustain populations. Landscapes could be assessed in a GIS by determining habitat configuration within each cell of a 2,000 ha uniform grid or within 2,000 ha windows placed randomly. Squares or circles would reasonably approximate the shape of pileated woodpecker territories in my study.

It is unlikely that pileated woodpeckers would continue to occupy recently logged landscapes unless there is retention of trees and snags in harvest areas and/or a component of stands of forest ≥7 m tall (approximately 30 years old) either interspersed within each 2,000 ha landscape or bordering it. My study did not determine the quantity of stands or substrates needed within a territory area to support a pair of pileated woodpeckers. However, the territories in my study contained about 200–600 potential cavity trees (≥30 cm dbh with stem decay) and 10,000–25,000 potential winter foraging substrates (≥20 cm dbh, dead trees or living trees with damage or decay). These ranges could be used as a conservative guideline for how much to leave standing as a combination of residual stands and structure in recently harvested areas. Converted to an average number of trees/ha, the ranges are 0.1–0.3 potential cavity trees/ha and 5.0–12.5 potential winter foraging substrates/ha. Locations of potential cavity trees and winter foraging substrates could be in stands within the territory and trees or clumps retained in harvested or tended areas. If known, existing cavity tree stands should be the highest priority for maintenance at the landscape scale.

I emphasize that it is possible, and I believe likely, that pileated woodpeckers could prosper in forest landscapes with lower quantities of potential cavity trees and foraging substrates than these estimates. I recorded successful reproduction in landscapes with <10% forest. To minimize risk, I recommend a minimum of 5% retention at the stand level in or bordering recently harvested areas of approximately 2,000 ha. Areas protected from harvesting for other purposes should be sufficient to meet pileated woodpecker habitat needs in most situations.

At the stand level, maintenance of potential cavity trees and foraging substrates in harvest areas and stand tending programs would help to conserve pileated woodpeckers. Trees containing existing cavities and basal foraging excavations have the highest value because cavity

trees and foraging sites are frequently reused by pileated woodpeckers. Cavity trees usually have extensive stem decay and low value for forest products. Living foraging trees usually have extensively honeycombed heartwood, excavated by carpenter ants, extending upward several meters from the base, which also reduces timber value. Hard snags and living trees with damage or decay also have good future potential as pileated woodpecker cavity trees or foraging substrates and lower timber value. Finally, any vertical structure retained in harvest areas should provide predator escape opportunities and may have future value for foraging. Following are specific recommendations about managing for pileated woodpecker cavity trees and substrates:

1. Protect existing cavity trees wherever they occur. The best way to do this is to provide forest workers with information on what kind of trees pileated woodpeckers use for cavity trees and what a pileated woodpecker cavity looks like. Cavities are typically 3–15 m above the ground on a branch-free portion of the trunk. The entrance is somewhat egg-shaped, widest at the bottom of the hole, and large enough for a human fist to fit into. Workers should be asked to look for cavity trees as part of their responsibilities and protect them when found, at either the planning or operations stage. Vary the approach to protecting cavity trees to maximize the probability that pileated woodpeckers and other species will continue to use them. This could range from protecting only the cavity tree to protecting a portion of the stand it is in, because pileated woodpeckers continue to use existing cavity trees that are retained in harvested areas.
2. Manage to provide future potential cavity trees, with a focus on the preferred species: trembling aspen and balsam poplar (*Populus balsamifera*). Coniferous species are acceptable where deciduous species are not abundant. Living trees that are already infected with heartrot fungus (visible conks) or with other external damage that may support current or future decay are the best, as they are likely to stand longer than dead trees and have little timber value. Large dead trees >7 m tall with broken trunks also have high potential value for pileated woodpeckers. Protect some stands that have or can be expected to develop large trees, especially trembling aspen that may become potential cavity trees. These should focus on deciduous or mixed stands in areas where deciduous species occur, particularly where deciduous species are relatively uncommon. To reduce risk of loss of cavity trees, I recommend a minimum of 5 stands ≥5 ha in size distributed in each 2,000 ha area. Living trees, with and without current decay, should also be retained in harvest areas to provide future potential cavity trees. Vary the approach from protecting single trees to clumps or patches. It is probably not necessary to retain potential cavity trees in all harvest areas, particularly if the pre-harvest stand does not contain deciduous species. Younger stands and trees that have been reserved as potential future cavity trees must be protected long enough to allow them to develop into trees large enough to meet pileated woodpecker needs.
3. Protect stubs, snags, and living trees in harvest areas that already have pileated woodpecker foraging excavations – these are used repeatedly by pileated woodpeckers. Train operators to recognize pileated woodpecker excavations and/or carpenter ant sawdust. Pileated woodpecker foraging sign is distinctive – look for rectangular holes, with the long axis oriented along the tree trunk, excavated 5 cm or more into the sapwood at the base of trees, with large wood chips about the size of a dollar coin. Also look for trees with fine sawdust at the base, which is dumped outside the tree by carpenter ants. Leave variable structures ranging from the foraging substrate or ant tree to small clumps of trees surrounding it. For mechanical harvesting operations, high-stump snags or living trees at or above 3 m high if desired to address safety concerns or recover merchantable wood volume. Focus on living trees and relatively sound dead trees for retention – wobbly and soft trees have higher safety concerns and lower short and long-term value as standing foraging trees for pileated woodpeckers.
4. Manage to provide future potential foraging substrates, with a focus on large trees and snags or younger living trees that will be left to grow larger, in both residual stands and future potential foraging substrates in harvest areas. To minimize risks of loss of individual stands, I recommend at least 5% retention of widely distributed residual stands at a landscape scale and an average of at least 2 trees/ha in harvested areas. As for cavity trees, it is probably not necessary to retain trees in all areas, and an approach to vary heterogeneity will probably

increase overall use. Retention or high-stumping is recommended for stems that have basal damage (fire scars, stem cracks) or other defects (conks, crook, etc) that lower merchantable value but provide high potential for future pileated woodpecker foraging. Protected understory trees may also develop into foraging substrates after several decades, well before regenerated trees develop to suitable condition.

5. Scattered foraging substrates may be of more value than clumped trees. Carpenter ant colonies each occupy a small area of forest and extra trees in a small area may not be used if ants defend their colony space. Ensuring wide distribution of trees may provide opportunities for more carpenter ant colonies. This strategy will also enhance broader use by pileated woodpeckers, which rarely foraged into openings more than about 50 m from standing trees.

It is important to consider future supply of cavity trees and foraging substrates in managed areas as well as the immediate future after harvesting occurs. Dead trees retained at harvest have high current value but may not stand for more than a decade. Living trees, which will continue to grow and die at different times until the next harvest, offer the best opportunity to ensure a continuing supply of cavity trees and foraging substrates. Trees and stands may be temporarily maintained to provide benefits and harvested at a future date or left to die naturally. The smallest territory in my study, which I believe represents high quality habitat, was in an area logged 40 years previously where living deciduous trees and understory white spruce had been left standing. The birds in this territory did not use the regenerated 40 year old trees, but they extensively used trees left standing after the logging and those that had since fallen. Most of the trembling aspen retained at harvest 40 years ago were very large and had extensive stem decay. This territory also had 41 cavity trees, which indicates that the territory had probably been occupied for many decades.

It is essential to maintain a component of dead wood in managed forests to maintain ecological function. Within that context, these pileated woodpecker conservation recommendations can be implemented with minimal impact on timber values. The best trees to retain for pileated woodpeckers include dead and damaged trees that have low timber value. Many forest managers already have dead wood conservation programs that could be adapted to increase their value for pileated woodpeckers.

Forest managers are concerned with conservation of all species as part of biodiversity conservation programs. I believe that conservation strategies designed to conserve pileated woodpeckers should also be beneficial for other species, particularly those that use tree cavities. However, strategies implemented for pileated woodpeckers will not necessarily be appropriate for other species, and managers should place them in context with other aspects of biodiversity conservation programs. My research has contributed new information to understanding of pileated woodpecker habitat ecology that can be used by managers as part of the continual improvement process.

PRIORITIES FOR FUTURE RESEARCH

My study suggests that pileated woodpeckers show flexibility in habitat selection and use and that they are able to maintain fitness across a habitat gradient. Further work is needed to determine habitat quantity and quality thresholds where fitness is reduced or territory viability is precluded. This will require radiotelemetry studies in areas with low amounts of forest cover or very young forests.

Research is also needed to investigate landscape-scale population structure and distribution of territories. Are there areas in forest landscapes that are not occupied by pileated woodpeckers, or do defended territories cover most of the landscape? How are non-territorial birds, including juveniles, spaced across the landscape if defended territories are the norm? Is there a population of non-territorial floater birds that exists within or between defended territories, and are these the birds that replace territorial birds that die? What happens to juvenile birds after they leave their parent territory? Are survival rates of juveniles over the long term sufficient to replace territorial birds that die?

My results suggest that territory size and location were stable over the study period. To ensure long-term conservation, information is needed to determine long-term stability of pair

territory size and location in response to changes in climatic factors and forest composition and structure, particularly changes associated with major disturbances such as forest fires and logging. Experiments documenting habitat use before, during, and after large-scale disturbances, particularly logging, are warranted.

I documented substantial use of pileated woodpecker cavities by other species. Additional work to investigate cavity use interrelationships between pileated woodpeckers and other species would help to improve understanding of the role of pileated woodpecker cavities in conservation of cavity-using wildlife communities.

Northern goshawks are the primary predator of pileated woodpeckers. Additional work to investigate interrelationships between pileated woodpecker and northern goshawks, particularly habitat factors that affect pileated woodpecker vulnerability, would provide information to improve habitat management strategies. Of particular interest is the possibility that pileated woodpeckers could escape goshawk predation risk by occupying landscapes with forest areas too low to support goshawks.

CONCLUSIONS

This study has contributed to scientific knowledge about pileated woodpeckers and also to management strategies to conserve pileated woodpeckers in managed Alberta foothills forests. The major conclusions are:

Pileated woodpecker habitat ecology in Alberta foothills forests

1. Pileated woodpeckers were habitat generalists at the territory and stand scales of selection and habitat specialists at the foraging substrate scale.
2. Pileated woodpeckers were reluctant to forage in open areas that were more than ~50 m from standing trees, which was probably a predator avoidance behavior.
3. Pileated woodpeckers foraged primarily on carpenter ants throughout the year, but foraging methods changed from excavation in hard wood in winter to gleaning on the surface and excavation into soft wood in the summer, probably because of food availability.
4. Pileated woodpeckers excavated nest and roost cavities in large trees with stem decay. They preferred living trembling aspen infected with heartrot fungus, especially *Phellinus tremulae*. Dead deciduous and coniferous species, especially trees with broken trunks, were also used.
5. Pileated woodpeckers selected trees with an "open space" around the entrances to nest and roost cavities that may be a predator avoidance behavior.
6. Pileated woodpecker cavities were an important resource for cavity-using wildlife species, and they may be a critical resource for large species that can not enter smaller woodpecker cavities.
7. Pileated woodpecker territories were more than 4 times larger in Alberta foothills forests than previously reported maximums.
8. The portion of the territory used during the nesting season was smaller than the overall territory area, suggesting that large territories are defended to secure sufficient food resources to ensure winter survival.
9. Despite large territories, productivity and adult survival rates were the highest ever reported for pileated woodpeckers.
10. There were significant relationships between 5 habitat quality variables and territory size. The best predictor of good habitat was the percent of stands that were ≥7 m tall.
11. Because habitat use was not closely linked to variables linked to mature and old forests, existing Habitat Suitability Models may be overly conservative and should be re-evaluated using pileated woodpecker research data.
12. Habitat variables and territory size were not related to fitness (productivity and survival), which was relatively stable across the habitat gradient investigated.

Pileated woodpecker conservation and management of forests

1. Pileated woodpeckers are not mature/old forest obligates and they do not appear to be currently at risk in the Alberta foothills. Current trends in forest management towards managing to maintain the resource of large dead trees should provide both foraging

substrates and cavity tree opportunities and help to prevent pileated woodpeckers from becoming at risk in future.

2. Pileated woodpecker prosperity may be a good ecological indicator for the maintenance of forest function related to growth, death, and decay of large trees.
3. Pileated woodpecker prosperity may be a good indicator for the conservation of cavity-using wildlife communities in the Alberta foothills and in other forests of similar tree species composition..
4. Existing pileated woodpecker cavity trees should be protected because of their relative rarity, low rate of replacement, and importance to pileated woodpeckers and other cavity-using wildlife.
5. Existing substrates with pileated woodpecker foraging excavations should be protected because they have high current and future value for pileated woodpeckers and low value for wood products.
6. Because pileated woodpecker pairs defend exclusive territories, an appropriate management scale for provision of habitat should approximate the average size of pileated woodpecker territories, about 2,000 ha. To support pileated woodpeckers through time, I recommend that, in each 2,000 ha landscape, managers should maintain at least 2% in stands with potential cavity trees and 5% in stands with potential foraging substrates. Potential cavity tree stands also qualify as potential foraging substrate stands. My research did not determine habitat quantity needed to conserve pileated woodpeckers, and these recommendations are based on my opinion.
7. In addition to existing cavity trees and foraging substrates, managers should retain additional trees and snags in harvested areas to provide future opportunities for pileated woodpeckers and to provide current predator escape opportunities that will allow pileated woodpeckers to exploit recently harvested areas. Density of potential cavity trees in territories was 0.1–0.3 trees/ha and density of potential winter foraging substrates was 5–12.5 trees/ha. These amounts represent conservative guidelines that can be used to increase the probability that pileated woodpeckers will continuously occupy managed forests.

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